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Investigations of luminance- and contrast-modulated binocular rivalry

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Gewidmet meiner Mutter

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Abstract

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Investigations of luminance- and contrast-modulated binocular rivalry

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Binocular rivalry can occur when incompatible stimuli are presented separately to the eyes. Since the invention of the stereoscope by Wheatstone in 1838, binocular rivalry has been intensively investigated with visual stimuli, which are differentiated from the background by variations in luminance, so-called luminance-modulated stimuli. However, it is also possible to perceive stimuli for which luminance of the target does not differ from that of the background but instead varies in contrast: so-called contrast-modulated (CM) stimuli. The main aim of this thesis is to investigate CM and noisy luminance-modulated (LM) stimuli under binocular rivalry conditions as the gained knowledge would enhance our understanding of both CM processing, as well as binocular rivalry. Perceptual change rates, proportions of exclusive visibility, mixed percepts (i.e. piecemeal and superimposition), as well as changes of these proportions across time and distributions of perceptual phases were calculated and compared between various CM and LM stimulus conditions. To compare those stimulus types with each other, the detection threshold was measured in one experiment to determine the visibility of each stimulus type, i.e. multiples above threshold. LM stimuli engage in significantly more exclusive visibility and trigger more alternation even when CM stimuli are of comparable visibility. Lower proportions of exclusive visibility and numbers of perceptual alternation for CM stimuli were due to greater proportions of superimposition. When comparably visible LM and CM stimuli compete with each other under binocular rivalry conditions, CM exclusive visibility predominates over LM exclusive visibility. Even if LM visibility is many times above CM visibility, LM stimuli never reach perceptual predominance. This result suggests that CM stimuli are processed unlike LM stimuli by neurones that receive initial binocular input. The results obtained were integrated into models concerning alternation dynamics and underlying processing sites for LM and CM stimuli.

Keywords: Binocular rivalry, contrast-modulation, luminance-modulation, piecemeal percepts, superimposed percepts, multistable percepts

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APNL = Adjacent pixel non-linearity
BOLD = Blood-oxygenation-level-dependent
CM = Contrast-modulated
CRT = Cathode-ray-tube
fMRI = Functional Magnetic Resonance Imaging
H = Horizontal
IT = Inferior temporal area of the brain
L = Noiseless luminance-modulated
LGN = Lateral geniculus nuclus
LM = Noisy luminance-modulated
MT = Middle temporal area of the brain
P = Piecemeal
S = Superimposition
STS = Superior temporal sulcus of the brain
V = Vertical
VEP = Visual Evoked Potentials
V1-7 = Visual cortex area 1- 7

Chapter 1- Literature review

1.1 Introduction to binocular rivalry

When an image seen by one eye is different to that seen by the other eye, perceptual competition can occur. This phenomenon is known as binocular rivalry (e.g. Wheatstone, 1838; Breese, 1899; Levelt, 1965; Blake, 1989). For a better understanding of what this means, the reader is invited to engage in a *Gedankenexperiment* (experiment carried out just in the mind). If a horizontal grating is presented to the left eye, but a vertical grating is presented to the right eye, for a short moment one grating will be perceived, whilst the other grating will be suppressed. Perception then alternates so that the suppressed grating becomes visible, whilst the formerly visible grating will be suppressed. During binocular rivalry not only do the two exclusively visible perceptual states alternate, but also different 'mixed' states in between those exclusive states arise. In the literature, these mixed states are usually referred to as 'piecemeal', 'mosaic-like' (e.g. von Helmholtz, 1867; Blake, 1989), 'superimposed' (e.g. Brascamp et al., 2006) and 'transparency' (Yang, Rose and Blake, 1992), the latter providing an impression of depth.

The reader may be able to experience binocular rivalry when he or she holds a finger in front of the gratings in Figure 1.1 (i.e. 30 - 40cm away from the page and between the gratings), focuses on the finger and then tries to overlap the perceived gratings in the background. This perceptual phenomenon will be the general topic of this thesis.

The stimulus conditions traditionally used to generate binocular rivalry alteration are either orthogonally orientated gratings (Figure 1A) or two incompatible images, e.g. face-house stimuli, which carry different chromatic and pattern information (Figure 1B). Diaz-Caneja (1928) (translated by Alais, O'Shea, Mesana-Alais, and Wilson, 2000) and Kovács, Papathomas, Yang, and Feher (1996) demonstrated that binocular rivalry also depends on the global context of the task (Figure 1C, D, respectively). When free-fusing the stimuli in Figure 1D, the reader may experience alternation between a completely visible monkey face and a jungle scene, which results from the interocular grouping of intermingled image parts. Figure 1E depicts a stimulus set up that generates perceptual transitions between phases of exclusivity that are perceived in a wave-like fashion (Wilson, Blake, and Lee, 2001).

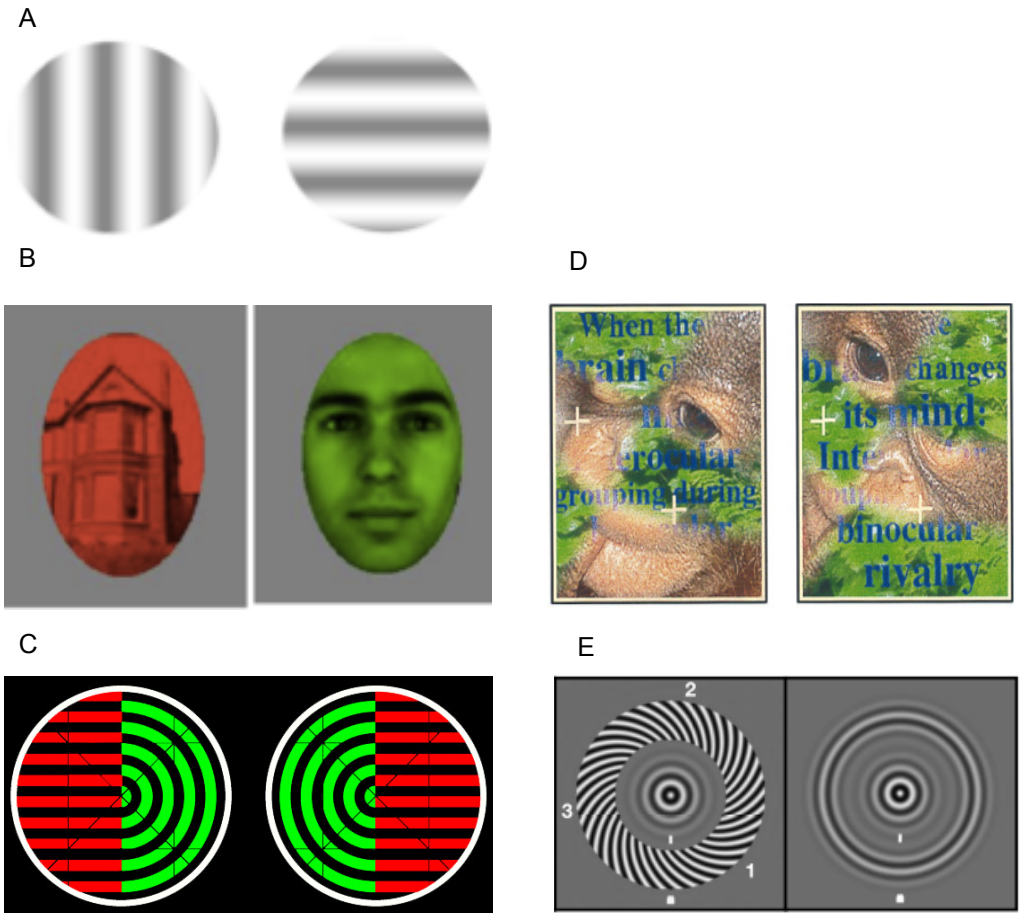


Figure 1.1: Variety of typical binocular rivalry stimuli. A) Orthogonally orientated gratings (created by the author) B) Red house versus green face stimuli (Alais, van Boxtel, Parker, and van Ee, 2010) C) Half of the rival stimulus contains a black-red grating, but the other half contains black-green semi-circles (Diaz-Caneja (1928) translated by Alais, O'Shea, Mesana-Alais, and Wilson, 2000), D) Portions of an image of a jungle and an image of a monkey are intermingled with each other, so that in addition to mixed percepts, exclusive monkey and exclusive jungle image can also be perceived (Kovács et al., 1996), E) A spiral grating and a concentric grating can initiate perceptual alternation, typically experienced as wave-like transitions across the actual percept (Wilson, Blake, and Lee, 2001).

1.1.1 Historical steps in binocular rivalry research

Binocular rivalry has been intensively investigated throughout past decades, but the first acknowledged report of it goes back to the 16th century. According to "*A Natural History of Vision*" by Nicholas Wade (1998), the first written report of binocular rivalry came from Porta (1593). He viewed two open books whilst his eyes were separated by a partition so that each eye looked at a different single page. At any one time, Porta could only read one page, which meant that the other page was suppressed. The perceptual dominance of one eye, and at the same time suppression of the other, demonstrates an important aspect of binocular rivalry. Centuries later, binocular rivalry was investigated systematically, after the revolutionary invention of the stereoscope, by Sir Charles Wheatstone in 1838 (Wheatstone, 1838). Wheatstone reported important characteristics of binocular rivalry, such as exclusive visibility of one eye's view whilst the other eye's view was suppressed, 'mixed' perception and alternation of those percepts. Moreover, Wheatstone claimed that voluntary will could not affect the length of dominance period, a statement, which initiated the on-going debate about the locus of binocular rivalry. In contrast to Wheatstone, Hermann von Helmholtz claimed to be able to hold a dominant percept just by an act of will. Whilst he viewed with one eye parallel lines in horizontal orientation and with the other eye parallel lines in vertical orientation, he described his perception as follow:

"... here I find that I am completely voluntary able to turn my attention soon to one and soon to the other line system, and that then this system will be seen alone and the other completely disappears." (Translated from the German original: von Helmholtz, 1867, page 770)

This observation would suggest that binocular rivalry is driven by a relatively high-level process. However, Ewald Hering disagreed with von Helmholtz's interpretation of binocular rivalry alternation because he could not influence the alternation of percepts by his will (Hering, 1920). Instead, Hering proposed that von Helmholtz's claim of voluntary alternation was due to small involuntary eye movements and local adaptation instead of voluntary attention. He argued:

"Anyways, Helmholtz has not considered the great meaning of the local adaptation and the eye movements for the mentioned rivalry phenomena and overestimated the influence of voluntary attention by far." (Translated from the German original: Hering, 1920, page 249)

It has been shown that saccades frequently occur before a perceptual change in binocular rivalry (van Dam and van Ee, 2006a). Although voluntary control by concentration and attention can affect the alternation process, it cannot completely stop perceptual changes (e.g. Lack, 1974).

The debate of where and how binocular rivalry is mediated is still on-going and will be a vital part of this thesis. Influential monographs about binocular rivalry research were published in 1899 and 1909 by Burtis Burr Breese (Breese, 1899, 1909). Instead of trying to explain the underlying reasons for the phenomenon of binocular rivalry, he aimed to systematically investigate the effects of stimulus characteristics on the perceptual alternation during binocular rivalry. He wrote:

"The object of my experiments was not so much to find an explanation for binocular rivalry, as to determine what conditions, both subjective and objective, affect it, and to what extent the phenomenon throws light upon the general problem of inhibition." (Breese, 1899, pages 20-21).

Breese investigated the number of perceptual changes, actual dominance duration, and averaged length of dominance duration over trials (Breese, 1909), which today are the standard metrics for binocular rivalry. He was also able to quantitatively assess the effect of 'strength' of a stimulus has on the characteristics of binocular rivalry. 'Strength' in that context meant luminance intensity. If the 'strengths' of both eyes' stimuli were the same, each stimulus predominated for approximately 50% of the trial time. The alternation rate increased when the luminance intensity of both stimuli was increased. Moreover, he first observed a phenomenon, which occurred when parts of a red and a green grating were superimposed in one eye with the aid of a prism (Breese, 1899). The superimposed parts did not fuse but gradually alternated, even though the perception of one colour was never exclusive. Breese called this perceptual phenomenon "monocular rivalry" (Breese, 1899, page 42). From then until the 1960s, the effect of stimulus characteristics were the subject of intensive investigations (e.g. Roelofs and Zeeman, 1919; Gellhorn and Schöppe, 1925; Gellhorn and Kuckenberg, 1924; Alexander, 1951; Alexander and Bricker, 1952).

The landmark dissertation *On binocular rivalry* from Levelt (1965) might be the most influential study concerning binocular rivalry. One important discovery of this work was the

connection between stimulus energy or as Levelt called it "stimulus strength" (Levelt, 1965, page 72) and the temporal characteristics of dominance and suppression phases during binocular rivalry. Levelt formulated four propositions or 'laws', which related the dynamics of binocular rivalry to stimulus characteristics (see Section *1.2.1 Exclusive visibility, predominance, mean duration and alternation rate*). Moreover, Levelt was the first to investigate the distribution of exclusively visible phases, which became a hallmark of binocular rivalry and other multistable perceptual phenomena (see Section *1.3 Distribution of exclusively visible phases*). Levelt's work was a turning point in binocular rivalry research because from then on, the binocular rivalry process was considered to be driven by stimulus characteristics such as luminance, luminance contrast, or colour contrast that are first encoded at an early or low-level of the visual cortex.

However, modern investigation techniques such as 1) visually evoked potentials (VEPs) (e.g. Lansing, 1964; Brown and Norcia, 1997; Wang, Gao, and Gao, 2004; Roeber and Schröger, 2004; Roeber, Veser, Schröger, and O'Shea, 2011; Kamphuisen, Bauer, and Ee, 2008; Jamison, Roy, He, Engel, and He, 2015), 2) functional magnetic resonance imaging (fMRI) (e.g. Lumer, Friston, and Rees, 1998; Polonsky, Blake, Braun, and Heeger, 2000; Lee and Blake, 2002; Lee, Blake, and Heeger, 2005; Knapen, Brascamp, Pearson, van Ee, and Blake, 2011; Bertolino, Ferraro, Nigri, Bruzzone, and Ghielmetti, 2014), 3) neurophysiological single cell measurements in animals (e.g. Logothetis and Schall, Jeffrey, 1989; Logothetis, 1998), 4) theoretical and computer models (e.g. Lehky, 1988; Blake, 1989; Pettigrew, 2001; Wilson, 2003; Tong, Meng, and Blake, 2006; Pastukhov and Braun, 2011), 5) disrupting local neural activity with transcranial magnetic stimulation (Pearson, Tadin and Blake, 2007), 6) measures of eye movements during binocular rivalry (e.g. van Dam and van Ee, 2006a, 2006b) and 7) new (Logothetis, Leopold, and Sheinberg, 1996) as well as re-discovered ways of initiating competition between dichoptically presented rivalrous stimuli (Diaz-Caneja (1928) translated by Alais et al., 2000; Kovács et al., 1996) throw new light on the old debate about whether binocular rivalry is a mainly low-level, high-level or an integrative process, which involves both processing stages.

Apart from its use as a tool in the search of correlates of visual perception, binocular rivalry has been used to quantify eye dominance (Handa et al., 2004) and for studying perception in bipolar disorders (Pettigrew and Miller, 1998; Miller et al., 2003; Nagamine, Yoshino, Miyazaki, Takahashi, and Nomura, 2009), autism (e.g. Robertson, Kravitz, Freyberg, Baron-

Cohen, and Baker, 2013; Freyberg, Robertson, and Baron-Cohen, 2015) and amblyopia (e.g. Schor, 1977; Lunghi, Morrone, Secci and Caputo, 2016).

1.1.2 Other multistable perceptual phenomena

In addition to the well-studied phenomenon of binocular rivalry, other ambiguous, bistable, or multistable percepts such as the Necker cube, Rubin's vase, monocular rivalry, plaid rivalry and apparent ambiguous motion, also generate perceptual ambiguity (De Marco, Penengo, and Trabucco, 1977; Leopold and Logothetis, 1999; Blake and Logothetis, 2002; Merk and Schnakenberg, 2002; Meng and Tong, 2004; Zhou, Gao, White, Merk, and Yao, 2004; Sterzer and Kleinschmidt, 2007) (Figure 1.2). These ambiguous percepts share some similarities with binocular rivalry such as the distribution of durations of dominant percepts (e.g. Borsellino, Marco, and Allazetta, 1972; Sterzer, Russ, Preibisch, and Kleinschmidt, 2002; Zhou et al., 2004; O' Shea, Parker, La, and Alais, 2009), dependence on stimulus strength (Klink, van Ee, and van Wezel, 2008), and areas of metabolic activity (Buckthought, Jessula and Mendola, 2011).

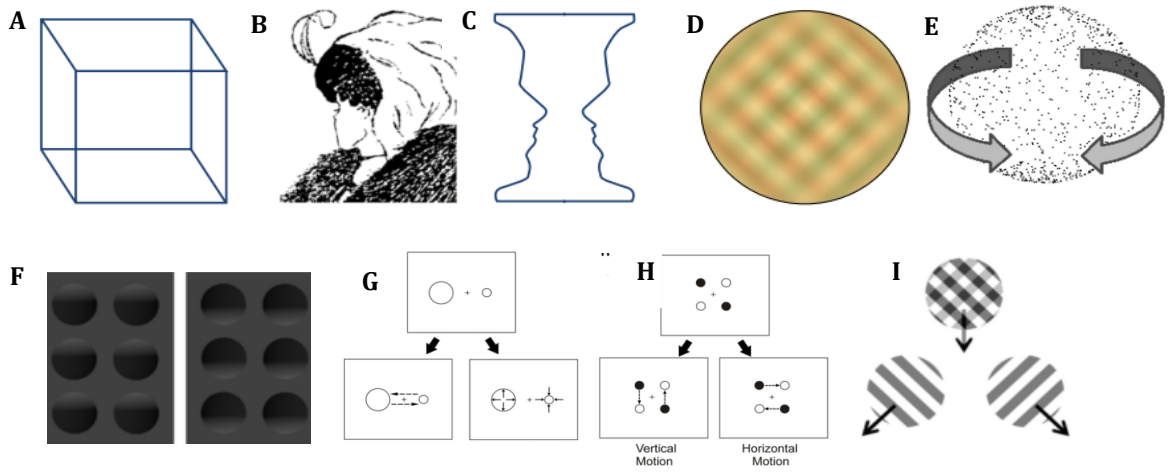


*Figure 1.2: Examples of multistable percepts. A) Louis Albert Necker (1786 * - 1861 †) famous optical illusion, called Necker's cube. Perceptual alternation between front- and backside of the cube occur. B) "Young girl- old women" illusion first published by an anonymous painter 1888 in Germany (Weisstein, 2016). Either an old or a young woman will be seen. C) The optical illusion "Rubin's vase" from the Danish psychologist Edgar John Rubin (1886 * -1951†). Either faces or a vase can be perceived. D) "Monocular rivalry" (e.g. Breese, 1899). One of the oblique gratings will be predominant and after a moment perception will alter to the oppositely orientated grating. E) If two-dimensional dots rotate in a certain order, a three-dimensional structure can be generated in the absence of any depth information, called "kinetic depth effect" (Wallach and O'Connell, 1953). The moving dots create a bistable structure-form-motion stimulus with rotation in either clockwise or anticlockwise direction. F) Shape from a perception of shading (Ramachandran, 1988). Assuming that light comes from above, depth information generates either a camber or dint. G) Ambiguous motion percept. An observer experiences either two dots exchanging positions or two dots expanding and contracting individually (Suzuki and Peterson, 2000; Scocchia, Valsecchi and Triesch, 2014). H) Apparent ambiguous dots motion. Two single dots presented successively with a constant frame rate create either vertical or horizontal motion perception (Wertheimer, 1912; Muckli et al., 2002; Scocchia, Valsecchi and Triesch, 2014). I) Another form of visual bistability is the perceptual change of moving plaids (Wallach 1976,1936). Here, the drifting plaid can be experienced as one single stimulus or as two gratings, which seem to be superimposed but in different depth planes. A-D taken from the original Blake and Logothetis (2002) paper, E-I taken from Scocchia, Valsecchi, and Triesch (2014).*

Other paradigms in which one stimulus is consistently seen by one eye whilst a flashed stimulus is presented to the other eye, also generate phases of exclusive visibility (e.g. Wolfe, 1984; Wilke, Logothetis and Leopold, 2003; Tsuchiya and Koch, 2005). For example, in the case of continuous flash suppression (e.g. Tsuchiya and Koch, 2005), a low-contrast stimulus is presented to one eye whilst the other eye views different, continuously flashed piecemeal images (Figure 1.3), often referred to as "*Mondrians*" in reference to the Dutch painter Piet Mondrian (1872 * - 1942 †). The phases of exclusive visibility are much longer and the threshold contrasts to detect a contrast increment in the suppressed eye (i.e. depth of suppression) were much higher during continuous flash suppression conditions compared to those of conventional binocular rivalry (Tsuctshiya, Koch, Gilroy and Blake, 2006). Hence, continuous flash suppression has been considered to be a specific perceptual phenomenon and not a special case of binocular rivalry.

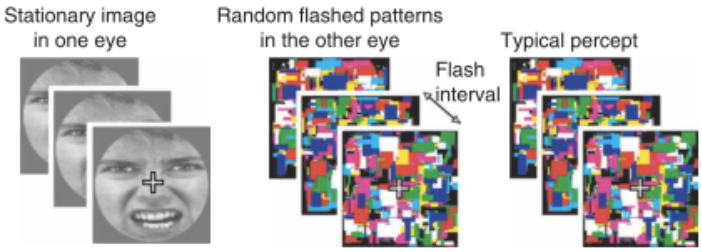


Figure 1.3: Scheme of a continuous flash suppression procedure. One eye views a static low-contrast image and the other eye views a high-contrast image with an on-off flash interval between 10 to 20 Hz. The percept of the flashed Mondrian is stable and appears for a much longer time than under conventional binocular rivalry conditions (Tsuchiya and Koch, 2005).

1.2 Hallmarks of binocular rivalry

Why does binocular rivalry occur? What is the underlying neuronal mechanism? What affects the dynamics of binocular rivalry? And finally, what can we learn from the perception during binocular rivalry about normal binocular vision? This review aims to address these questions. To begin with, the next section focuses on the hallmark characteristics of binocular rivalry.

1.2.1 Exclusive visibility, predominance, mean duration and alternation rate

Since Breese (1899), temporal measures of perceptual phases and changes have become standard in the investigations of binocular rivalry. Perceptual phases, in which one of the rival stimuli is visible in its entirety, or at least predominantly visible and at the same time the opposite stimulus is suppressed in its entirety, or at least predominantly suppressed, are referred to as *exclusive visibility* (e.g. O'Shea, Sims, and Govan, 1997), *predominance* (e.g. Levelt, 1965), *perceptual exclusivity* (Knapen et al., 2007) or *perceptual dominance* (e.g. Blake, 2001). However, the neural locus may differ when a percept is *exclusively* or just *predominately* visible. For example, Polonsky, Blake, Braun, and Heeger (2000) used a predominance paradigm in a neuro-imaging study, in which the participant had to indicate single grating perception when the grating was visible for ≥75% of the entire percept. Strictly speaking, this could be either a mixed or an exclusively visible percept. On the other hand, Knapen et al. (2011) used a paradigm for their neuro-imaging study, in which the participants were asked to indicate either exclusive visibility or mixed percepts. Comparisons of these data can be misleading as a mixed percept might engage in different processing areas than exclusively visible percepts do (see Section *1.2.2.1.1 Neural locus of piecemeal percepts*). Hence, it is best to ask participants to indicate when exclusively visible percepts are seen to avoid possibly confounding of data.

Another characteristic of binocular rivalry is the rate at which one exclusively visible (or predominant) percept alters to the other exclusively visible percept across a defined period of time, often referred to as the *rate of fluctuation* (Breese, 1909), *alternation rate* (e.g. Levelt, 1965), *rivalry alternation* (Blake, 1977), *rivalry rate* (O'Shea et al., 1997) or *perceptual flips* (van Dam and van Ee, 2006b).

The total time of exclusive visibility divided by the alternation rate gives the average duration of exclusively visible percepts, which has been referred to as the *average length of phase* (Breese (1909), *mean nonsuppression phase duration* (Fox and Rasche, 1969), *mean rivalry dominance duration* (Lehky, 1995), *rivalry period* (O'Shea et al., 1997) or *mean dominance duration* (e.g. Bossink, Stalmeier, and De Weert, 1993).

Exclusive visibility (or predominance), alternation rate and mean exclusivity (or dominance) duration have been lawfully connected with physical stimulus attributions by Levelt (Levelt,

1965; Brascamp et al., 2015). As already highlighted in the Section *1.1 Introduction to binocular rivalry,* Levelt's work is of great importance for the study of binocular rivalry as he formulated propositions, which allow predictions to be made about perceptual characteristics of binocular rivalry if 'stimulus strengths' are known. Stimulus strength refers to the physical stimulus property, which determines the ability of one eye's stimulus to suppress the other (e.g. contrast, luminance intensity, interocular orientational differences, colour contrast). Levelt's original laws are formulated as follows:

"I. Increase of the stimulus strength in one eye will increase the predominance of the stimulus.
II. Increase of the stimulus strength in one eye will not affect the average dominance duration for the same eye.
III. Increase of the stimulus strength in one eye will increase the alternation frequency.
IV. Increase of the stimulus strengths in both eyes will increase the alternation frequency." (Levelt, 1965, page 76)

Since their introduction, the laws have been intensively studied (e.g. Fox and Rasche, 1969; Bossink, Stalmeier and De Weert, 1993; Klink, van Ee and van Wezel, 2008). Modifications to Levelt's original laws have been made to take into account the vast body of experimental results and the modified four laws were recently published in a review that celebrated the 50th anniversary of the original work (Brascamp et al., 2015) as:

"I. Increasing stimulus strength for one eye will increase the perceptual predominance of that eye's stimulus.
II. Increasing the difference in stimulus strength between the two eyes will primarily act to increase the average perceptual dominance duration of the stronger stimulus.
III. Increasing the difference in stimulus strength between the two eyes will reduce the perceptual alternation rate.
IV. Increasing stimulus strength in both eyes while keeping it equal between eyes will generally increase the perceptual alternation rate, but this effect may reverse at near-threshold stimulus strengths." (Brascamp et al., 2015, page 27)

Specifically, the second, third and fourth law have been modified because of the limited range of stimulus conditions used in Levelt's original work. The original second law suggested that when one eye's stimulus strength is fixed and the other eye's stimulus strength is varied, then the mean exclusivity duration of the fixed-eye's stimulus is unaffected by the changes. It is noteworthy that Levelt based this proposition on findings, in which he used a fixed-eye-stimulus with relatively high stimulus contrast (i.e. stimulus strength). The modified second law takes into account that some later investigations demonstrated a slight but significant reduction of the mean exclusivity duration of the fixed-eye's stimulus (e.g. Mueller and Blake, 1989; Bossink, Stalmeier and De Weert, 1993). Also, results of some studies showed that the mean exclusivity duration of the fixed-eye's stimulus changes if this stimulus strength is relatively low (e.g. Brascamp et al., 2006; Kang, 2009). The original third law predicted that an increase of one eye's stimulus strength will increase the alternation rate. However, the modification of the second law makes the third law's prediction obsolete. In fact, the modified third law predicts that the alternation rate decreases with increasing difference in stimulus strength between the eyes. Moreover, the peak alternation rate will be reached when both stimulus strengths are equal. The original fourth law states that the increase of both stimulus strengths will increase the alternation rate. The modified fourth law specifies that both stimuli's strengths need to be equal in the eyes to lead to an increase of the alternation rate and addresses possible limitations around near-threshold contrast levels.

These laws have been used to explain the characteristics of both binocular rivalry but also other multistable perceptual phenomena (e.g. Klink et al., 2008 but see also review Brascamp et al., 2015).

1.2.1.1 Neural locus of exclusive visibility

It is still a matter of debate whether phases of exclusivity and predominance are processed in early visual cortex, at later levels of the visual pathway, or perhaps in both stages. Researchers used neuro-imaging technology to search for the locus of exclusive visibility.

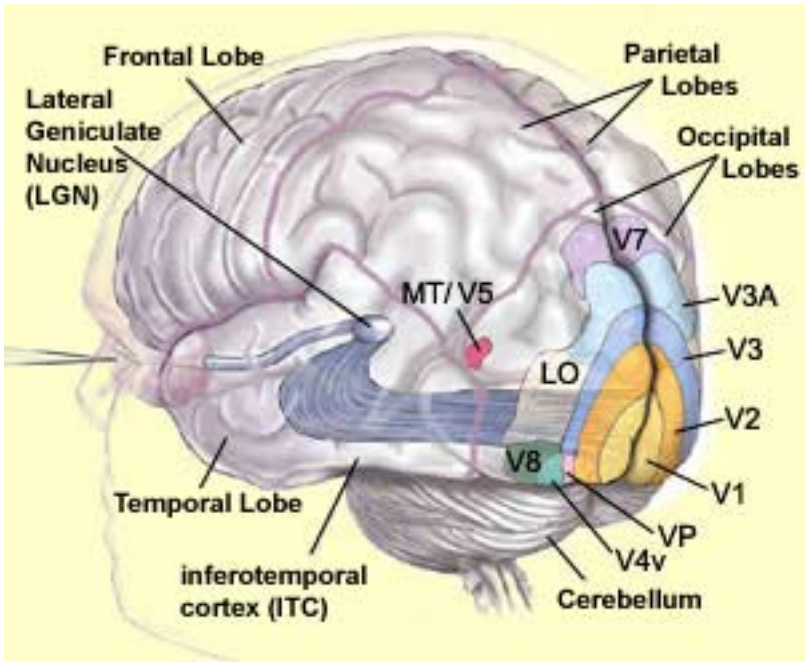


Figure 1.4: Scheme of a human brain and its relevant visual processing regions taken from Dubuc (2017).

Tong, Nakayama, Vaughan, and Kanwisher (1998) initiated rivalry with separately presented green face and red house stimuli whilst measuring the metabolic fluctuations in fusiform face area (FFA), which responds specifically to faces in comparison to non-face stimuli (Kanwisher, McDermott and Chun, 1997) and the parahippocampal place area (PPA), which responds strongly to houses and places but not to faces (Epstein and Kanwisher, 1998). Stimulus-selective metabolic activation was found in both cortical regions (FFA activity increased when a face was seen, PPA activity when a house was seen). Moreover, the results were not significantly different to a control condition, in which either house or face stimuli presented monocularly, alternated between the eyes. This finding led the researchers to the conclusion that the competitive neural interaction must have been resolved by the time the visual input reached the areas FFA and PPA.

Polonsky and collaborators (2000) investigated blood-oxygen-level-dependent (BOLD) activity in V1, V2, V3, V3a, V4v whilst initiating binocular rivalry with orthogonally presented low-contrast red and high-contrast green gratings. The contrast of the gratings differed by an approximate factor of 4, with the high contrast grating presented to the dominant eye of each participant, to ensure long dominance periods. The BOLD activity in V1, as well as nearby areas (V2, V3, V3 and V4v), tended to increase when the high contrast grating was seen and decreased when the low contrast grating was seen. The researchers

proposed that the neural events underlying binocular rivalry are due to firing of V1 neurones, but Polonsky and co-workers did not rule out the possibility that events in later stages of the visual pathway could have also contributed to the measured V1 activity via feedback.

Wunderlich, Schneider, and Kastner (2005) used methods similar to those of Polonsky et al. (2000), but with a focus on the lateral geniculate nucleus (LGN) and V1. The researchers reported that exclusive visibility was correlated with BOLD activity in LGN and V1. Also, the activity was slightly higher in V1 than in LGN. Also, Wunderlich and co-workers demonstrated higher metabolic activity in LGN and V1 when a participant perceived a high-contrast grating and lower activity when a low-contrast grating was perceived. Wunderlich and co-workers concluded that early visual areas are strongly involved in exclusive visibility during binocular rivalry. The researchers suggested that LGN's activity was due to interactions within LGN or from feedback from V1.

Haynes, Deichmann, and Rees (2005) also reported BOLD activity in LGN and V1 during binocular rivalry. The researchers then used rotating grating stimuli to initiate dominance phases during binocular rivalry and investigated BOLD fluctuations in LGN and V1. Both brain areas showed a strong increase of metabolic activity during dominance phase and strong reduction of activity to eye-specific LGN regions when a stimulus was perceptually suppressed. The researchers did not investigate nearby visual areas but concluded that binocular rivalry is processed as early as LGN. As noted already by Wunderlich, Schneider, and Kastner (2005), activity in the LGN might be due to internal interactions or feedback signals from V1.

A fMRI study addressing the question of whether dominant or exclusive percepts are mediated in early or later stages of the visual pathway was conducted by Tong and Engel (2001). The researchers measured metabolic fluctuation during binocular rivalry in area V1. Tong and Engel presented a grating to one eye's blind spot and its surrounding area and another grating to the other eye's corresponding ipsilateral area. Participants reported perceptual dominance and mixed perception via button presses whilst BOLD activity was measured in V1. The blind-spot area in the cortex receives input only from the ipsilateral eye. The researchers found that perceptually dominance corresponded with metabolic activity in V1. These responses were as strong as under conditions in which monocular gratings were

physically alternated between the eyes. Hence, Tong and Engel suggested that binocular rivalry is resolved in the monocular visual cortex.

Lee and Blake (2002) measured metabolic activity in V1 during exclusive visibility using grating and object stimuli and compared the findings with results from control conditions, using monocular alternation of single gratings and monocular alternation of single grids. The researchers demonstrated a first experiment that V1 activity was highest under the grid stimulus conditions and lowest with the single grating conditions. Under binocular rivalry conditions, V1 activity was lower than the grid condition, but higher than the grating condition, implying that suppression caused the higher activity than the physical alternation of monocularly presented gratings. Areas V2, V3 and V4 showed comparable results: under rivalry condition, the BOLD activity was higher than that for single gratings but lower than for the grid condition. In a second experiment, the results for V1, V2, V3 and V4 were repeated with object (i.e. house and face) stimuli. Lee and Blake demonstrated with this work that rivalry suppression occurs as early as V1 regardless of whether grating or meaningful stimuli have been used.

Buckthought et al. (2011) carried out a study to compare BOLD signals between monocular and binocular rivalry. The researchers generated binocular rivalry with dichoptically presented red and green gratings and varied the contrast (9%, 18%, 36%). Participants indicated predominance (here over two-thirds or more of the entire percept) by pressing keys. Buckthought and collaborators reported that during predominance phases, the cortical areas V1, V2, V3, V3A as well as the inferior parietal cortex near the temporoparietal junction, superior parietal cortex, lateral occipital regions, middle and inferior frontal cortex, premotor cortex and supplementary motor area showed activity. Interestingly, and of significance for the current review, is that BOLD activity was strongest in V1-V3. Also, a strong signal was found when using 38% contrast, a reduced signal strength when using 18% contrast, but higher signal strength when using 9% contrast. The researchers speculated that the reason for the increase of signal strength for 9% contrast conditions was at least partly due to a release of suppression because of the lower alternation rate, but also due to higher attentional resources, which may be necessary to distinguish between low-contrast gratings.

Authors of a study concerning motion stimuli under binocular rivalry conditions investigated BOLD activity when exclusive visibility was generated using moving colour dots

(Moutoussis, Keliris, Kourtzi and Logothetis, 2005). One eye's dots were moving randomly (noise) whereas 50% of the other eye's dots moved in one direction. Moutoussis and collaborators showed that BOLD activity is linked to area V5, known to be specialised in motion perception, but also area V3, V3A, and LOC. No differences in responses were found between noise and coherent motion in the areas V1, V2, and V4. This means that the stimulus properties, such as motion, determine also, which area of the visual processing is initially activated during exclusive visibility.

A recent publication (Eklund, Nichols, and Knutsson, 2016) revealed that the software packages frequently used for the analysis of results from fMRI studies were based on erroneous statistical assumptions and contained code errors, resulting in reports of statistically significant BOLD activity, which in fact was not significant.

A direct way to localise neuronal activity in the primate brain is single cell recording. The principal idea is to implant microelectrodes into certain brain areas of interest. Neurones are the fundamental unit of processing in the brain; they transmit information via electrical signals due to changes in voltage called 'action potentials'. Microelectrodes are placed within or close to cell membranes and measure the rate of action potentials across time, for different visual stimuli. Single cell studies in monkeys during binocular rivalry have been conducted (for a review of these studies see Logothetis, 1998). Very few V1/V2 neurones were activated during dominance and suppression phases in trained monkeys, whilst area V4 showed higher activity during suppression (Leopold and Logothetis, 1996). Another result of a study with untrained monkeys showed no significant difference in action potentials in V1 and LGN between rival and non-rival conditions (Lehky and Maunsell, 1996). Finally, strong action potentials could be measured in later stages of the visual pathway, namely superior temporal sulcus (STS) and the inferior temporal cortex (IT) (Sheinberg and Logothetis, 1997). These results suggest that binocular rivalry alternation is a result of competition between neurones, which receive initial binocular input. The single cell findings differ considerably from those of results of fMRI studies. Reasons for these discrepancies were discussed by Polonsky et al. (2000). The researchers suggested that species differences, uncontrolled eye movements, uncertainties of interpretation of the BOLD activity and strength of the neuronal output (Logothetis et al. 2001), possibly underestimated representations of single cell activity compared to the average of a larger field of neurones in the visual cortex, measured by fMRI

technology. Logothetis and co-workers also highlighted the possibility that mixed perceptual stages that occur between exclusive states may have confounded the single-cell results.

Despite the growing literature on binocular rivalry and the growing body of neuro-imaging studies, it is still not clear where exclusivity during binocular rivalry is processed. Many results of fMRI studies have shown that alternation of exclusive (and predominant) percepts correlates with alternation of metabolic activity as early as V1 (Tong and Engel, 2001; Lee and Blake, 2002) or even LGN (Wunderlich, Schneider and Kastner, 2005; Haynes, Deichmann and Rees, 2005) (although possibly due to feedback). Also, meaningful stimuli (e.g. faces and house) show neural correlates during binocular rivalry dominance phases as early as V1 (Lee and Blake, 2002) and gratings even in the LGN (Haynes, Deichmann and Rees, 2005; Wunderlich, Schneider and Kastner, 2005) whereas exclusivity evoked by motion (coherent moving dots) initially generated BOLD activity in V3, V3A and V5 (Moutoussis et al., 2005). Results from single cell studies have challenged the view of an early processing site for binocular rivalry since perceptual alternation evoked measurable responses from only a few neurones in the early visual cortex, but more in later brain regions (Logothetis, 1998a).

The results of the studies outlined above will be further discussed in Section *1.4 Models and theories of binocular rivalry* as they contribute to the on going debate of where and which mechanism is responsible for binocular rivalry alternation. The processing sites of the different perceptual states are very important for models and theoretical frameworks of binocular rivalry and therefore, they will be key to this thesis. However, the paradigm, which generates perceptual states, is also of great importance in the context of binocular rivalry research. Hence, the next two sections will focus on particular cases of exclusive visibility, namely inter- and intraocular grouping and 'flicker-swap-rivalry'. These types of exclusivity were generated under different stimulus conditions than exclusivity generated under conventional stimulus conditions. Different brain regions may be involved in these types of exclusivity and therefore they play a significant role in the understanding of binocular rivalry processing.

1.2.1.2 Special cases of exclusivity during binocular rivalry: Interocular and intraocular grouping

Interocular grouping or pattern rivalry represents a special case of an exclusively visible percept during binocular rivalry. For a better understanding, the reader is encouraged to revise Figure 1.1C and 1.1D to experience interocular grouping.

Diaz-Caneja (1928) report translated by Alais et al. (2000) was the first to describe the observation that under some conditions, rivalrous stimuli, containing portions of two images, can be perceptually combined to produce the perception of a complete image. As depicted in Figure 1.1C, Diaz-Caneja used stimuli that contained intermingled portions of two images presented to each eye, a black-red horizontal grating and a black-green circular striped pattern. Diaz-Caneja noted that most of the time, despite the rivalrous nature of these stimuli, either a complete horizontal grating or a complete circular striped pattern was seen. Also, he noted that the alternation between complete images was more achievable when closing the eyes and perceiving afterimages. Hence, even though the initial observation of interocularly combined percepts suggested the involvement of a 'high-level' mechanism, he proposed that binocular rivalry required both high level and low levels of visual processing. He noted that rivalry was more predominant for afterimages, which have "…lesser influence of attention" (Diaz-Caneja (1928) translated by Alais et al., (2000), page 1444). Diaz-Caneja's work provided substantial contribution to the debate about whether or not the competition observed during binocular rivalry arises between early areas of the visual processing or between areas that process higher cognitive information. Unfortunately, this study was left out of the academic focus until Logothetis' (1998b) rediscovery.

Decades later, Kovács et al. (1996) showed, without the knowledge of Diaz-Caneja's work, that the pattern itself can rival (Figure 1.1D). The researchers demonstrated interocular grouping for both object (monkey face and a jungle scene) and simple chromatic rivalrous stimuli (green and red dots). Also, Kovács and co-workers found that the distributions of phases of interocularly grouped percepts were not significantly different from those of exclusive percepts generated under conventional binocular rivalry conditions. On the contrary, the mean interocularly grouped durations were longer and the proportions of interocular grouping were lower than exclusively visible percepts under conventional

binocular rivalry conditions. The researchers treated interocular grouping equivalent to (conventional) binocular rivalry and suggested that binocular rivalry (including interocular grouping) "...might occur beyond input layers of the visual cortex" (Kovács et al., 1996, page 15511).

Kovács et al.'s (1996) view that interocular grouping is a higher level process have been also challenged by later investigations from a number of researchers (e.g. Alais and Blake, 1999; Stuit, Paffen, van der Smagt and Verstraten, 2011). The experiments from Alais and Blake (1999) were conducted to investigate the effects of intraocular grouping on binocular rivalry. Two grating stimuli presented to one eye in circular apertures were either 'collinear' (two horizontal gratings, to the left and right of a central fixation cross, or two vertical gratings, above and below the fixation cross, 'parallel' (two horizontal gratings, above and below a central fixation cross, or two vertical gratings, to the right and left) or 'orthogonal'. The circular apertures presented to the other eye were filled with a static noise pattern. Some of the stimuli are shown in Figure 1.5. Participants had to indicate via key presses, which grating was visible. The time when both gratings were visible simultaneously (so-called "joint predominance" (Alais and Blake, 1999, page 4343)) was highest under the 'collinear' conditions and lowest under orthogonal conditions. In a second experiment, the contrast was varied between the gratings. The joint predominance was highest when the contrasts were equal and lowest when they were different. Another finding was that the joint predominance decreased when the separation between the rival gratings (under the same conditions as in the first experiment) increased. These results demonstrate that exclusivity of a single rival zone depends on the input of adjacent zones but that this dependency is spatially limited. This would be in line with a previously proposed idea that exclusivity during binocular rivalry develops in small adjacent zones across the visual space (Blake, O'Shea and Mueller, 1992). Alais and Blake proposed that this dependency was limited by the spatial magnitude of cooperating, adjacent cells in V1.

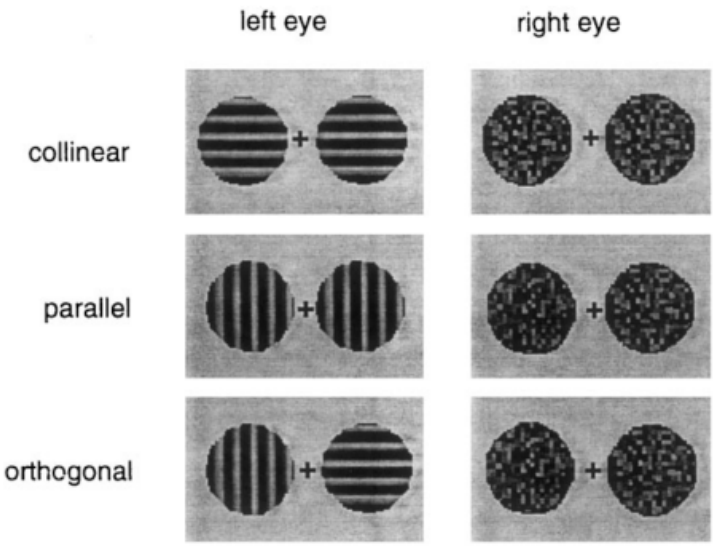


Figure 1.5: Scheme of stimulus conditions for one experiment of Alais' and Blake's (1999) paper.

Stuit, Paffen, van der Smagt, and Verstraten (2014) further investigated Alais' and Blake's (1999) idea, but used sinusoidal grids, gratings, and face stimuli to induce binocular rivalry. The stimulus conditions also included arrangements, in which matching images were presented to different eyes, to investigate interocular grouping (Figure 1.6.B, D, F, H). The underlying idea was that if joint predominance (i.e. grouping) is affected by higher-level processing of faces then a difference between results for face stimuli and for grid or grating stimuli would arise. However, as the results revealed, the joint predominance did not vary with stimulus type. The researchers suggested the image content affects grouping during binocular rivalry at an early, monocular stage of the visual pathway. Stuit and collaborators proposed a model, which categorises grouping as a result of inter- and intrahemispheric neuronal connections within early visual cortex.

In summary, it has been suggested that grouping during binocular rivalry is mediated by a higher level process, beyond the early visual cortex (Kovács et al., 1996), however, later results of a study concerning grouping proposed that grouping may be mediated within a low-level processing stage (Stuit, Paffen, van der Smagt and Verstraten, 2014).

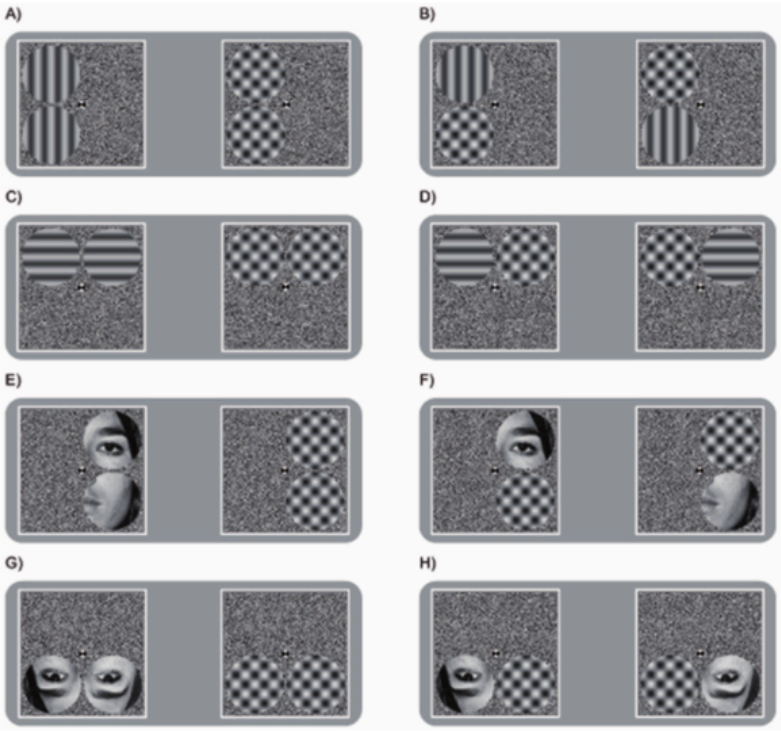


Figure 1.6: Stimulus conditions of Stuit's et al. (2014) experiments.

1.2.1.3 Special cases of exclusivity during binocular rivalry: Exclusivity during flicker-swap-rivalry

Another particular type of exclusive visibility that occurs during the so-called flicker-swap-rivalry, developed by Logothetis et al. (1996), contributed to the debate of whether binocular rivalry is a high or a low level process. The 'flicker' in this context refers to orthogonally orientated gratings, which were flickered synchronously in each eye at 18 Hz (i.e. gratings were flashed for 27.7 ms and separated by a blank screen presented for 27.7 ms). The 'swap' refers to an exchange of stimuli between the eyes every 333ms. The 'flicker' was used to minimise awareness of these stimulus swaps whereas the stimulus swap was used to eliminate the eye-of-origin information. Logothetis and collaborators compared the new paradigm to one where the orthogonal gratings were flickered, but not swapped, to address the question of whether neurones with an eye-of-origin information compete with each other (at an early stage in the visual pathway) or whether later, pattern representing processing regions mediate binocular rivalry. The researchers found that the flicker-swap-rivalry and the control conditions generated comparable phase distributions, well fitted with a gamma function, a hallmark of binocular rivalry (e.g. Levelt, 1967; Alais and Blake, 2005; Brascamp et al.,

2015). Also, the researchers tested the influence of unilateral contrast changes and demonstrated that both conditions produced results in line with previous findings (e.g. Levelt, 1965; Bossink et al., 1993; Brascamp et al., 2015). Logothetis and co-workers suggested that binocular rivalry alternation is mediated not by a conflict of monocular neurones in the early visual cortex, but instead in later processing stages, which represent patterns and suggested that these regions are the same as those processing other multistable percepts such as Necker's cube or monocular rivalry.

Flicker-swap-rivalry only holds for a limited range of stimulus conditions (Lee and Blake, 1999; see also Bonneh, Sagi, and Karni, 2001). Also, binocular rivalry generates significantly deeper suppression than flicker-swap-rivalry (Bhardwaj, O'Shea, Alais and Parker, 2008). Results from an fMRI study (Buckthought, Fesi, Kirsch and Mendola, 2015) demonstrated that flicker-swap-rivalry showed weaker activation in all brain regions than conventional binocular rivalry and generated mainly activity in higher ventral regions of the brain. The finding that weaker activity in earlier, but stronger activity in later visual stages led to the suggestion that flicker-swap-rivalry is a weaker version of binocular rivalry, lacking robust feed-forward signals from the early visual cortex.

In summary, the stimulus paradigm used is likely to affect the processing site of exclusively visible percepts. Whilst conventionally exclusive visibility seems to be processed in visual areas as early as V1 and LGN, grouping during binocular rivalry and exclusivity during flicker-swap-rivalry may have a processing site that initially engages higher visual areas.

In the experiments presented in this thesis, I use the conventional paradigm to initiate binocular rivalry with orthogonally orientated gratings.

1.2.2 Mixed perception

Early studies of binocular rivalry focused mainly on the perceptual dominance or suppression phases without giving much consideration to mixed percepts that may occur during transitions between exclusively visible percepts (e.g. Breese, 1899, 1909; Levelt, 1965; Fox and Rasche, 1969; Blake, 1977; Blake, Westendorf, and Overton, 1980). Contemporary binocular rivalry scholars have demonstrated a growing interest in the understanding of mixed perceptual states because of their different psychophysical characteristics and potential to reveal different underlying neuronal processing mechanisms than those of exclusive percepts (e.g. Liu et al., 1992; Yang et al., 1992; Brascamp et al., 2006; Knapen, Brascamp, Pearson, van Ee, and Blake, 2011). In fact, several types of mixed periods may occur during binocular rivalry (Figure 1.6), which will be explained and discussed in the following section.

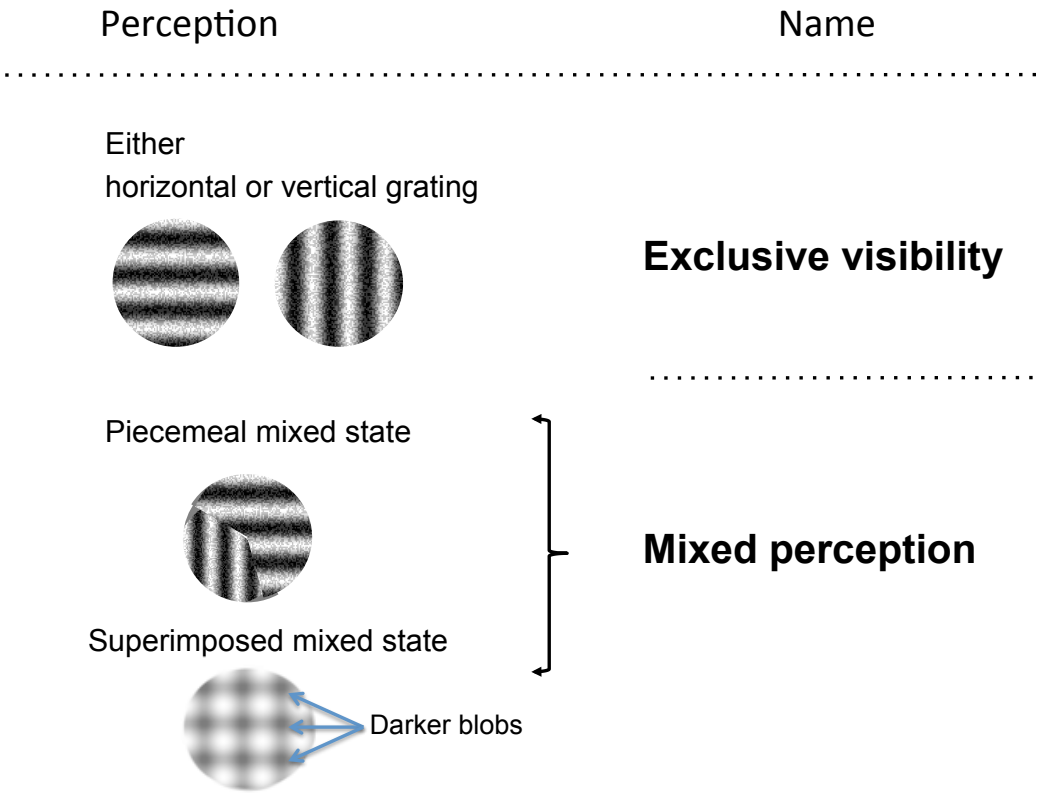


Figure 1.7: Scheme of the various perceptual states generated by dichoptically presented and orthogonally orientated sinusoidal gratings. An exclusively visible state occurs when only one grating is seen for a certain time whilst the opposite grating is absolutely suppressed. Mixed states can be subdivided into a 'piecemeal' mixed state, in which portions of each grating can be seen at the same time, and a 'superimposed' mixed state in which rivalrous low contrast gratings are fused, indicated by the blobs at the intersections.

1.2.2.1 Piecemeal perception during binocular rivalry

When non-overlapping portions of both rival stimuli are partially visible across the visual field of the entire percept, terms like 'piecemeal' (e.g. Blake, 1989), 'transitions' (e.g. Brascamp et al., 2006), 'patchwork rivalry' (e.g. Blake, 2001), 'mosaic-like' (von Helmholtz, 1867), 'composite of two stimuli' (Hollins and Hudnell, 1980), or 'mixture' percepts (e.g. Whittle, 1965; Klink, Brascamp, Blake, and van Wezel, 2010) have been used to describe this particular state of mixed perception. The term 'piecemeal' shall be used in this thesis. Piecemeal perception is considered to be rivalry in local zones across the visual field (Blake, O'Shea, and Mueller, 1992). Blake et al. (1992) introduced a model of spatial zones of rivalry, in which dominant percepts are generated by adjacent, non-overlapping retinal areas, which interact with each other. The authors wrote about mixed perception:

"During binocular rivalry each zone signals exclusive visibility from one eye or the other; a single zone cannot assume a mixed dominance state. The mixture of portions of left- and right-eye images that often occurs during rivalry results from the spatial concatenation of multiple zones that are in different monocular states." (Blake et al., 1992, page 475).

A special case of piecemeal perception during binocular rivalry relates to the so-called 'travelling waves' (Wilson et al., 2001). To initiate these travelling waves, a spiral is presented to one eye and a radial grating to the other eye. Perceptual alternation between exclusively visible states is typically perceived as a gradual, wave-like transition phase. This gradual, wave-like change from one exclusive state to another is supportive for the idea that piecemeal perception is an alternation of exclusively visible stimulus portions in local zones, which are adjacent and non-overlapping, but interacting with each other.

1.2.2.1.1 Neural locus of piecemeal percepts

The results of neuro-imaging studies have shown that mixed perception during binocular rivalry activates various areas of the brain (Lumer et al., 1998; Lumer and Rees, 1999; Polonsky et al., 2000). Lumer et al. (1998) and Lumer and Rees (1999) presented a red drifting grating to one eye and a green face to the other eye. Whilst perceptual alternations were indicated by key presses, metabolic activity in the brain was measured. The activity in the primary visual cortex was not significantly affected during mixed perceptual states. Support for no significant activity in V1 during mixed perception also comes from a study (Polonsky et al., 2000), in which the researchers presented dichoptically red and green gratings to participants eyes and measured metabolic responses in V1. The researchers found that the activity measured in V1 was not significant during piecemeal phases, but during physical transition phases, implying that V1 is not mediating piecemeal percepts (even if there was no significant difference between physical and alteration of exclusive percepts either). The authors suggested that (piecemeal) transitions reflect transitions of activity between the neural columns processing exclusive percepts, rather than being an own perceptual state. Unfortunately, Polonsky and co-workers did not investigate other visual brain areas, which would have given an answer to the question of whether later visual areas are more active during transition phases.

The findings from another study have shown that parietal and frontal areas of the brain do show an increase in metabolic activity during piecemeal mixed states (Lumer et al., 1998). Knapen et al. (2011) measured BOLD activity during mixed phases of binocular rivalry initiated with orthogonal gratings. The researchers found transition-related activity primarily located in the right hemisphere, beyond early visual cortex V1.

Both increases and decreases of BOLD activity in V1 have been reported to occur during perception of travelling waves transitions (see Section *1.2.2.1 Piecemeal perception during binocular rivalry*) (Lee et al., 2005). Some results of fMRI studies have shown no significant changes of BOLD activity during transient phases (Lumer et al., 1998; Lumer and Rees, 1999; Polonsky et al., 2000) whilst travelling-wave related fMRI results (Lee et al., 2005) did show changes in V1 activity. This discrepancy could mean that piecemeal perception has both an early and a later processing site, interconnected via feedback. Alternatively, it might mean

that travelling waves denote a further perceptual state during binocular rivalry, activating different visual areas to those activated by conventional piecemeal perception.

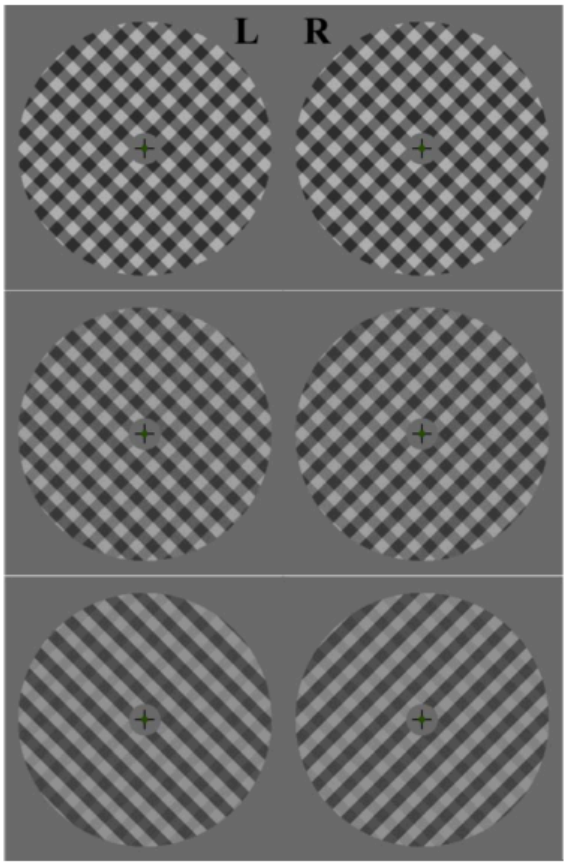


Figure 1.8: Stimuli used for Katyal et al.'s (2016) experiment.

In a recent electrophysiological study, Katyal et al. (2016) measured VEPs during binocular rivalry. The stimuli, made of superimposed, orthogonally orientated gratings, were presented dichoptically to each eye. The grating components of the grids varied in contrast (Figure 1.8). The stimuli flickered at different frequencies whilst VEPs were measured. The researchers investigated particularly frequencies that were combinations of the two input frequencies, so-called 'intermodulations', which can only be evoked by binocular neurones. The researchers found that both the two single frequencies and the intermodulation were predominately observed at electrodes close to the primary visual cortex. Importantly and of significance for this thesis, Katyal and co-workers found peak amplitudes of intermodulations during phases of mixed perception. This result suggests that mixed percepts may arise from binocular neurones.

1.2.2.2 Superimposed perception during binocular rivalry

When both rivalrous stimuli are simultaneously and entirely visible across the visual field (e.g. Liu et al., 1992), the terms 'superimposition' (e.g. Brascamp et al., 2006) or in the case of grating stimuli 'dichoptic plaid' (e.g. Liu et al., 1992) are used to describe this mixed perceptual state. The term 'superimposition' shall be used in this thesis. Yang, Rose, and Blake (1992) also described a particular superimposed state in which the two gratings overlapped each other, but one of the rival stimuli appeared to be in front of the other, which the researchers called "transparency" (Yang et al., 1992, page 47). A noteworthy observation in the context of depth perception during binocular rivalry was made by Schor who carried out a study concerning binocular rivalry and strabismic suppression (Schor, 1977). He used grating stimuli to initiate binocular rivalry alternation. The participants had to indicate whether they have seen an exclusive or mixed percept. In one experiment, he varied the interocular orientation difference and noted that participants with normal vision reported verbally that mixed percepts were perceived "...inclined in depth" (Schor, 1977, page 587) when small interocular differences (10 deg to 22.5 deg) were used whereas greater orientation differences generated superimposition with a depth impression.

Superimposed perception is thought to be an indicator for binocular combination and fusion (Liu et al., 1992; Brascamp et al., 2006). Gratings near contrast detection threshold level tend to combine instead of alternating (Liu, Tyler and Schor, 1992) and Liu and co-workers proposed that a separate neural mechanism is responsible for this 'dichoptic plaid'. Brascamp et al. (2006) investigated the characteristics of superimposed and piecemeal perception during binocular rivalry and the influence of different contrast levels (low to high) on these perceptual states. After a 10 s trial, the participants had to score the amount of mixed perception on a scale from 1 'only superimposed binocular rivalry' to 5 'only piecemeal binocular rivalry' (Figure 1.9). The occurrence of piecemeal perception decreased, and superimposition increased, with decreasing stimulus contrasts. As there was a gradual increase of superimposed perception as the contrast changed from approximately 50% to near detection threshold, Brascamp and co-workers questioned Liu et al.'s (1992) explanation of a separate processing mechanism being responsible for the superimposed stable, fused percepts near detection threshold. Such a mechanism would probably result in an abrupt end of piecemeal percepts when contrast is reduced to near detection threshold. Instead, Brascamp et al. (2006) suggested that binocular rivalry could be described as "…a gradual evolution"

(Brascamp et al., 2006, page 1251), implying that a percept changes from exclusive visibility to piecemeal and then to superimposed perception when reducing the stimulus contrasts.

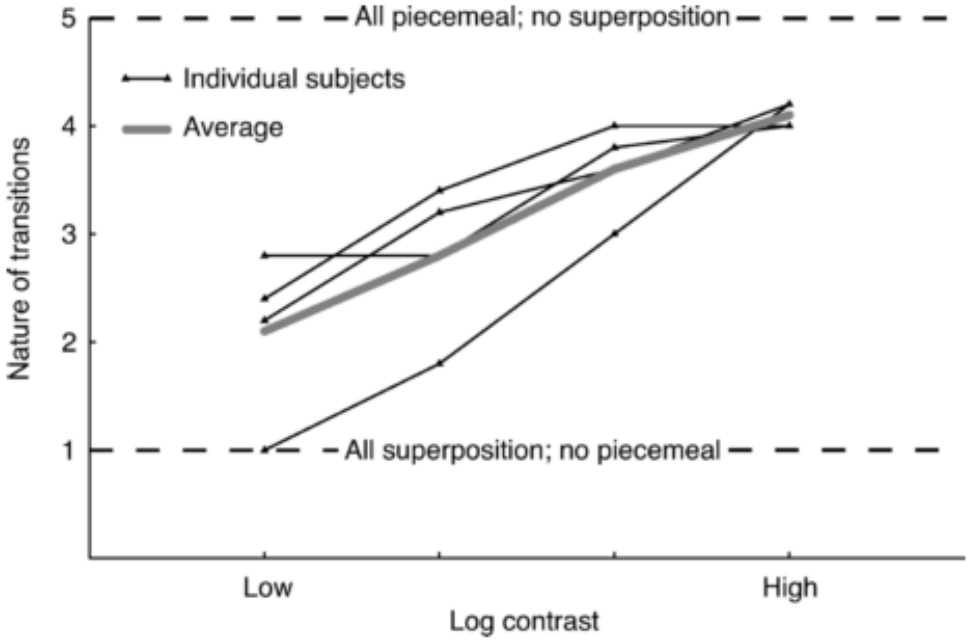


Figure 1.9: Judgment of piecemeal and superimposition as a function of contrast (Brascamp et al., 2006).

Burke, Alais, and Wenderoth (1999) presented orthogonally orientated, gratings to each eye with spatial frequencies ranging from 1 c/deg - 9 c/deg and contrasts from 5 % to 85 % (Figure 1.10). Participants had to judge whether they perceived exclusive visibility, piecemeal or superimposition. At a contrast level of 5%, all stimuli (1-4c/deg) showed only superimposition. In agreement with Brascamp et al.'s (2006) study, as the stimulus contrast increased, the general trend was for the proportion of percepts judged as fused plaids to decrease.

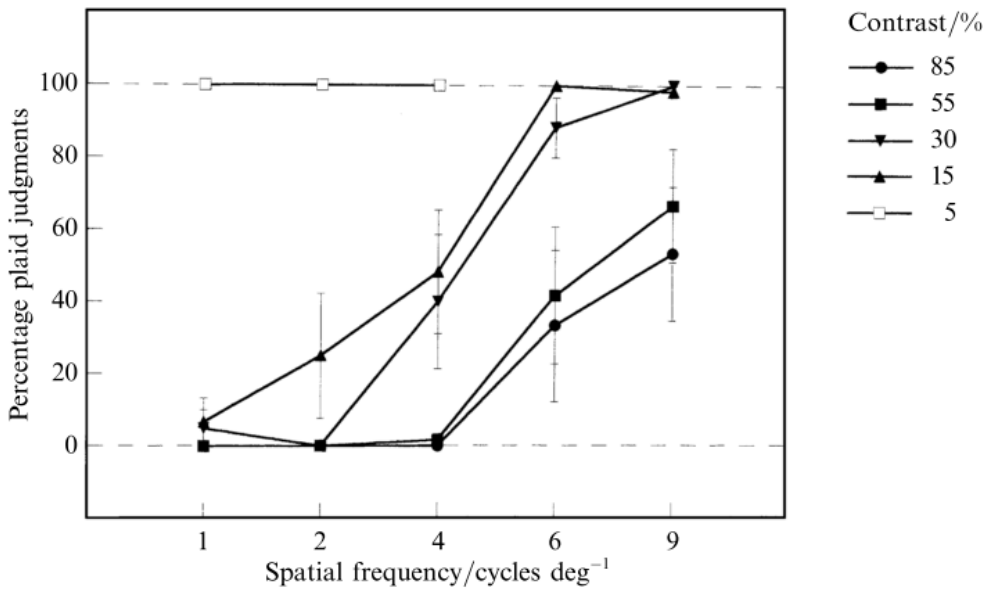


Figure 1.10: Fused perception as a function of spatial frequency and contrast (Burke, Alais, and Wenderoth, 1999).

Researchers who used fMRI technology to investigate binocular rivalry suggested that 'mixed' or 'transient' phases involve later, binocular stages of the visual pathway compared to those involved in the perception of exclusively visible percepts (Lumer, 1998; Lumer and Rees, 1999; Polonsky et al., 2000). However, the authors of those studies did not distinguish between piecemeal and superimposed perception during binocular rivalry. It might be possible that superimposed mixed percepts activate certain areas of the cortex due to a fusion mechanism and also due to possible binocular summation that may occur at the intersections of gratings perceived as superimposed, which can appear darker or lighter than the rest of the gratings, reported by Liu et al. (1992).

1.2.2.3 Perceptual changes and reversions during mixed states

As already noted in Section *1.2.1 Exclusive visibility, predominance, mean duration and alternation rate*, one measure of binocular rivalry is alternation rate between two exclusively visible states. However, mixed percepts that can occur between phases of exclusive visibility will influence this parameter. Goldstein and Cofoid (1965) were the first to include alternation from an exclusively visible percept to a mixed state when the researchers described the rate of "perceptual changes" (Goldstein and Cofoid, 1965, page 236) in their study. Perceptual changes from a dominant percept to a mixed state and back again to the previously seen

dominant percept have also been observed and have been referred to as ‘compound phase’ (Mueller and Blake, 1989), ‘return transitions’ (Brascamp et al., 2006) or ‘reversion’ (Robertson et al., 2013). The term reversion shall be used in this thesis.

The existence of reversions has implications on the general understanding of the underlying neuronal mechanism of binocular rivalry as will be discussed in Section *1.4 Models and theories of binocular rivalry*. Paraan, Bakouie, and Gharibzadeh (2014) pointed out that terms such as ‘transition’ or ‘transient phase’ in the context of mixed phases during binocular rivalry can be misleading as the researchers suggest that a mixed state is only a stage in-between two dominant phases. However, reversions also occur during binocular rivalry (Mueller and Blake, 1989; Brascamp et al., 2006) and therefore, Paraan and colleagues (2014) suggested that mixed percepts are *“*...not a mere bridge connecting the two dominant states, but a state which dominates consciousness randomly*...”* (Paraan et al., 2014, page 5). This statement gets support from results of neuro-imaging studies, which showed that several regions of the brain are active during mixed phases but inactive during phases of exclusive visibility (Lumer et al., 1998; Polonsky et al., 2000; Knapen et al., 2011).

Following Brascamp et al.'s (2006) idea of a gradual development of binocular rivalry, it would be reasonable to expect that the perceptual alternations that involve mixed states follow the same pattern, i.e., a superimposed percept is more likely to change to a piecemeal state rather than changing immediately to exclusively visible state. So far, no experiments have investigated this aspect of perceptual changes during binocular rivalry.

1.2.2.4 Clinical applications for mixed perception during binocular rivalry

Binocular rivalry has been used as a clinical tool to investigate patient populations with abnormal neuronal processing properties, e.g. amblyopia, autism or bipolar disorder (Schor, 1977; Holopigian, Blake, and Greenwald, 1988; Karen Holopigian, 1989; Nagamine et al., 2009; Robertson et al., 2013; Freyberg, Robertson, and Baron-Cohen, 2015; Lunghi, Morrone, Secci, and Caputo, 2016). As well as monitoring exclusive visibility during binocular rivalry, the amount of mixed perception can be used as a metric to demonstrate differences in visual processing between those patient groups and control populations.

Autistic patients show longer phases of mixed perception compared to control groups (Robertson et al., 2013) regardless of whether rivalling object stimuli or orthogonally orientated gratings are used (Freyberg, Robertson and Baron-Cohen, 2015b). Also, moderate and heavy social drinkers show an increase of mean piecemeal duration during binocular rivalry after alcohol consumption (Cao et al., 2016a).

A number of studies concerning binocular rivalry and amblyopia have been carried out (Holopigian, Blake, and Greenwald, 1988; Karen Holopigian, 1989; Lunghi, Morrone, Secci, and Caputo, 2016), but only Schor (1977) reported results of mixed percepts. He found that non amblyopic participants showed longer phases of mixed perception when the interocular orientation difference between the gratings was small (10 deg to 22.5 deg). Importantly, the non amblyopic participants also reported verbally that under these conditions, mixed percepts were perceived with an impression of depth, which led Schor to the suggestion that visual levels, which process stereopsis, are activated during this particular condition. On the other hand, the results of strabismic participants indicated shorter mixed phases under the same stimulus conditions, which led Schor to the suggestion that binocular rivalry conditions, which involve stereopsis in normal vision, may initiate suppression in strabismus. However, it is unclear what the contribution of superimposition and piecemeal to the total proportion of mixed perception was.

Lunghi et al. (2016) used binocular rivalry to test the plasticity of amblyopic children. Orthogonally orientated gratings were used to initiate binocular rivalry. The experimental set-up and task were children-friendly. The children had to indicate verbally the dominance of either grating orientation before (baseline) and after start of the occlusion therapy (range: 2 hours, 1, 2, and to 5 months). The mean dominance duration was then calculated. The predominance of the non-amblyopic eye was boosted 2 hours after on-set of the occlusion therapy. Interestingly, the increase of dominance of the non-amblyopic eye was correlated with an increase of visual acuity in the amblyopic eye after 2 months of treatment. Lunghi and co-workers suggested that the increase of dominance in the non-amblyopic eye shortly after the beginning of the occlusion therapy could be used for monitoring amblyopia treatment. Lunghi and co-workers did not include the indication of piecemeal perception in their paradigm, as they were aware that such task would be rather difficult when children are asked to indicated their perception. The children were asked after the experimental session whether they experience patchwork percepts, but none of the children reported such percepts. I

speculate that this was due to the small stimulus sizes and relatively high contrasts, which are both known to decrease proportions of mixed percepts (e.g. Blake, O'Shea and Mueller, 1992; Klink, Brascamp, Blake and Wezel, 2010b; Brascamp et al., 2006). However, it might be that the disrupted binocularity in amblyopes additionally diminished the proportions of mixed percepts.

All clinical populations mentioned above may provide suitable candidates for investigations of superimposed percepts during binocular rivalry since superimposition is thought to be an indicator for binocular fusion (e.g. Brascamp et al., 2006; Liu et al., 1992) and areas of binocular fusion may be particularly disrupted under some clinical conditions (bipolar disorder, autism, anxiety) but unambiguously for other clinical conditions (after heavy alcohol consumption and amblyopia).

1.3 Distribution of exclusively visible phases

The temporal characteristics of exclusively visible percepts during binocular rivalry are known to be well fit by a gamma distribution (e.g. Levelt, 1965; Zhou et al., 2004; Brascamp and Ee, 2005). This 'binocular rivalry hallmark' (Alais and Blake, 2005; O' Shea et al., 2009) was first observed and described by Levelt (1965, 1967). As shown in Figure 1.12, the number of events (y-axis) are typically plotted against the trial duration (x-axis), either individually or normalised across trials and participants. The distribution of events demonstrates a rapid increase of phase durations and then decreases gradually in a right-skewed fashion. Levelt speculated that randomly distributed "excitation spikes" (Levelt 1965, page 94) in the brain are necessary to evoke exclusive visibility and thought that eye-movements are associated with those spikes. Figure 1.11 shows events of exclusive visibility for two individuals. The length of those events varies randomly across time for the participants, as one would expect if excitations spikes occur randomly. Additional support for this idea come from results of a study by van Dam and van Ee (2006a), who demonstrated that perceptual alternation is correlated with eye movement (van Dam and van Ee, 2006a).

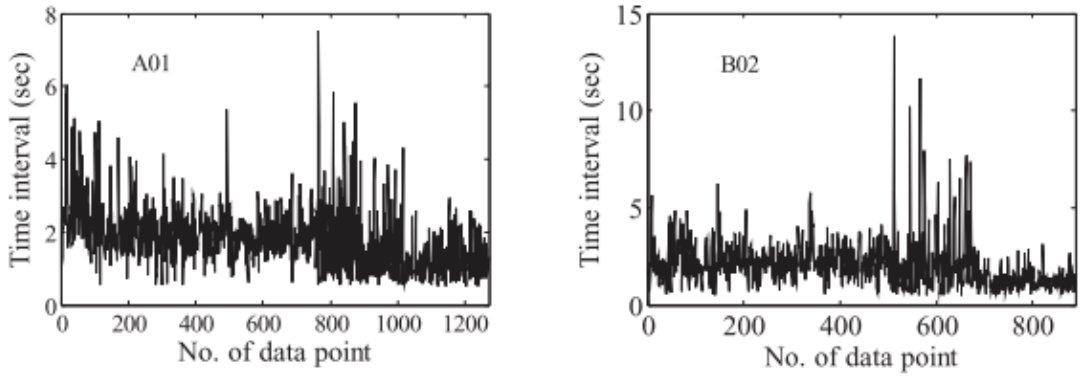


Figure 1.11: Example tracks of exclusively visible phases. Y-axis represents the length of exclusively visible events and the X- axis shows the number of exclusively visible events for two participants (Zhou et al., 2004).

Other distributions may also represent the numbers of exclusively visible phases during binocular rivalry (Cogan, 1973; Lehky, 1995; Zhou et al., 2004; Shpiro, Moreno-Bote, Rubin, and Rinzel, 2009). Cogan (1973) was the first who systematically studied different theoretical distributions, namely gamma, lognormal, Weibull, exponential and normal distributions. Using the chi-square test for goodness of fit, she found a high resemblance between the various distributions, which was later confirmed by scholars of other studies (Lehky, 1995; Zhou et al., 2004). She subdivided the perceptual categories into exclusively visible percepts and several mixed forms, which were either partial perception of both orthogonally, orientated line stimuli (piecemeal) or full perception of both stimuli (superimposition). Whilst piecemeal rivalry seemed to fit the same distributions as exclusively visible percepts, superimposed percepts did not occur very often and showed no specific pattern.

Other multistable percepts show a gamma-like distribution as well (e.g. Borsellino, De Marco, Allazetta, Rinesi, and Bartolini, 1972, De Marco, Penengo, and Trabucco, 1977; Kleinschmidt, Buchel, Zeki, and Frackowiak., 1998; Carter and Pettigrew, 2003; Murata, Hamada, Kakita, and Yanagida, 2004; Pastukhov and Braun, 2008; O' Shea et al., 2009). The fact that the gamma function suitably fit distributions of exclusive visibility for different multistable perceptual phenomena were thought to be a measure of a common underlying processing mechanism (e.g. Murata et al., 2004; Zhou et al., 2004; O' Shea et al., 2009). However, the potential meaning of a gamma-fit phase duration data has also been placed in

doubt (Arnold, 2011). Brascamp and Ee (2005) demonstrated that the distribution of alternation rates can also be fit with a gamma function. The quality of the fit showed better results than those for the exclusively visible phases. The authors argued that the prominent role of the gamma phase distribution in the binocular rivalry literature is not justified by its quality compared to alternation rate distributions.

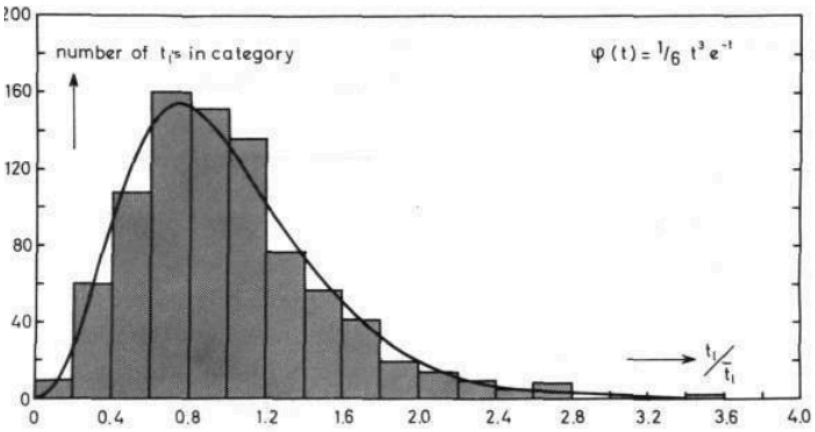


Figure 1.12: Typical distribution of exclusively visible phases during binocular rivalry. Y-axis represents the number of exclusively visible events and the x- axis shows the duration of exclusively visible percepts. The superimposed function depicts a gamma function (Levelt, 1965).

The following equation represents the function that is used to fit perceptual phases:

$$f(x|\alpha,\beta) = \frac{1}{\beta^{\alpha}\Gamma(\alpha)}\, x^{\alpha-1} e^{\frac{-x}{\beta}}\ ; x > 0, \alpha > 0, \beta \geq 0$$

The gamma function is indicated with $\Gamma(\alpha)$, the 'shape' parameter is α and represents the skewness of the distribution, the 'scale' parameter β scales the distribution along the abscissa and the number of perceptual events x (e.g. Levelt, 1965; Veser, O'Shea, Schröger, Trujillo-Barreto, and Roeber, 2008; O' Shea, Parker, La, and Alais, 2009).

1.4 Models and theories of binocular rivalry

A fundamental aim of binocular rivalry research is to understand the processes that underlie this phenomenon and then to implement these processes into a framework. Modelling is a powerful tool to connect underlying processing mechanisms of perceptual alternation with experimental findings by creating simplified metaphorical schemes or mathematical models. In the following section, the theories and underlying models of binocular rivalry shall be discussed to address two main questions: where are the neuronal loci for the different percepts, which can occur during binocular rivalry and what are the underlying mediating mechanisms for the perceptual alternations?

1.4.1 Eye-rivalry and pattern-rivalry

One widely accepted idea is that alteration during binocular rivalry results from mutual inhibition (e.g. Blake, 1989; Kang and Blake, 2011; Seely and Chow, 2011) between monocular neurones in the visual cortex V1 (reviewed and summarised by Blake, (1989)) or LGN (Lehky, 1988). This proposal is also known as interocular competition or the eye-rivalry theory (e.g. Lee and Blake, 1999; Leopold and Logothetis, 1999; Tong, 2001). As already stated in an earlier Section (see Section *1.2 Hallmarks of binocular rivalry*), results of psychophysical (e.g. Blake, 1989), electrophysiological (e.g. Katyal et al., 2016) and neuro-imaging (Tong and Engel, 2001; Lee and Blake, 2002) studies suggested that exclusive visibility during binocular rivalry is resolved in the V1. Some results of fMRI studies also suggested the involvement of the LGN (Haynes, Deichmann and Rees, 2005; Wunderlich, Schneider and Kastner, 2005). Under some stimulus conditions, phases between an alternation from one exclusive percept to another can appear as a wave-like transition (see Section *1.2.2 Mixed perception*), which correlates with an increase in metabolic activity in V1 (Lee et al., 2005). On the other hand, several other results of neuro-imaging studies also demonstrated activity of various higher areas during mixed states (Lumer et al., 1998; Knapen et al., 2011).

Another theory is that binocular rivalry is a product of competition between dissimilar patterns rather than competition between the eyes and therefore a higher cognitive process. Logothetis et al.'s (1996) flicker-swap-rivalry paradigm generates perceptual alternation, which cannot be explained by eye-based competition of monocular neurones and was thought

to be a product of competing binocular areas (see Section *1.2.1.3 Special cases of exclusivity during binocular rivalry: Exclusivity during flicker-swap-rivalry*). This result was supported by an fMRI study, which demonstrated that flicker-swap-rivalry showed weaker activation in earlier brain regions than conventional binocular rivalry and generated mainly activity in higher ventral regions of the brain (Buckthought et al., 2015). Another case of possible pattern rivalry is observed during interocular grouping (see Section *1.2.1.2 Special cases of exclusivity during binocular rivalry: Interocular and intraocular grouping*) since an entire percept cannot be generated by purely monocular neurones only (Diaz-Caneja (1928) translated by Alais et al., 2000; Kovács et al., 1996; Stuit et al., 2011). Additional support for the 'higher-level processing theory' comes from neurophysiological results of studies in monkey (see Section *1.2.1.1 Neural locus of exclusive visibility*) as binocular rivalry did not evoke significant activity in LGN or V1 (Lehky and Maunsell, 1996; Leopold and Logothetis, 1996), but instead strong action potentials were found in later stages of the visual pathway, namely superior temporal sulcus (STS) and the inferior temporal cortex (IT) (Sheinberg and Logothetis, 1997).

It is of interest that visual attention, a higher cortical process, also contributes to binocular rivalry (see review Paffen and Alais, 2011). For example, it has been shown that voluntary control can influence the alternation of percepts during binocular rivalry (e.g. Lack, 1974; Meng and Tong, 2004; van Ee, van Dam, and Brouwer, 2005). Eye movements might also influence the alternation of perception since saccades occur just before a perceptual change (van Dam and van Ee, 2006b).

The hybrid model proposed by Tong et al. (2006) (Figure 1.13) includes various types of neuronal connections, which might underlie different binocular rivalry characteristics. Figure 1.13A shows a simplified model of mutual inhibition of monocular neurones and binocular neurones (blue lines with a filled circle). Grouping during binocular rivalry could be explained by mutual excitatory connections between neurones in adjacent regions of the visual space, represented with two yellow and green blocks (Figure 1.13B). Importantly, each set of neurones receives inputs from both eyes. In the case of mutual excitation of monocular neurones, eye-based competition could involve inhibition that occurs between monocular neurones tuned to different orientations. Also, interocular grouping between neurones with similar orientation preference or excitatory connections between pattern-selective binocular neurones can generate grouping across adjacent regions. Excitatory feedback could account

for inhibition of pattern-selective neurones, selective attention as well as grouping during binocular rivalry (Figure 1.13C).

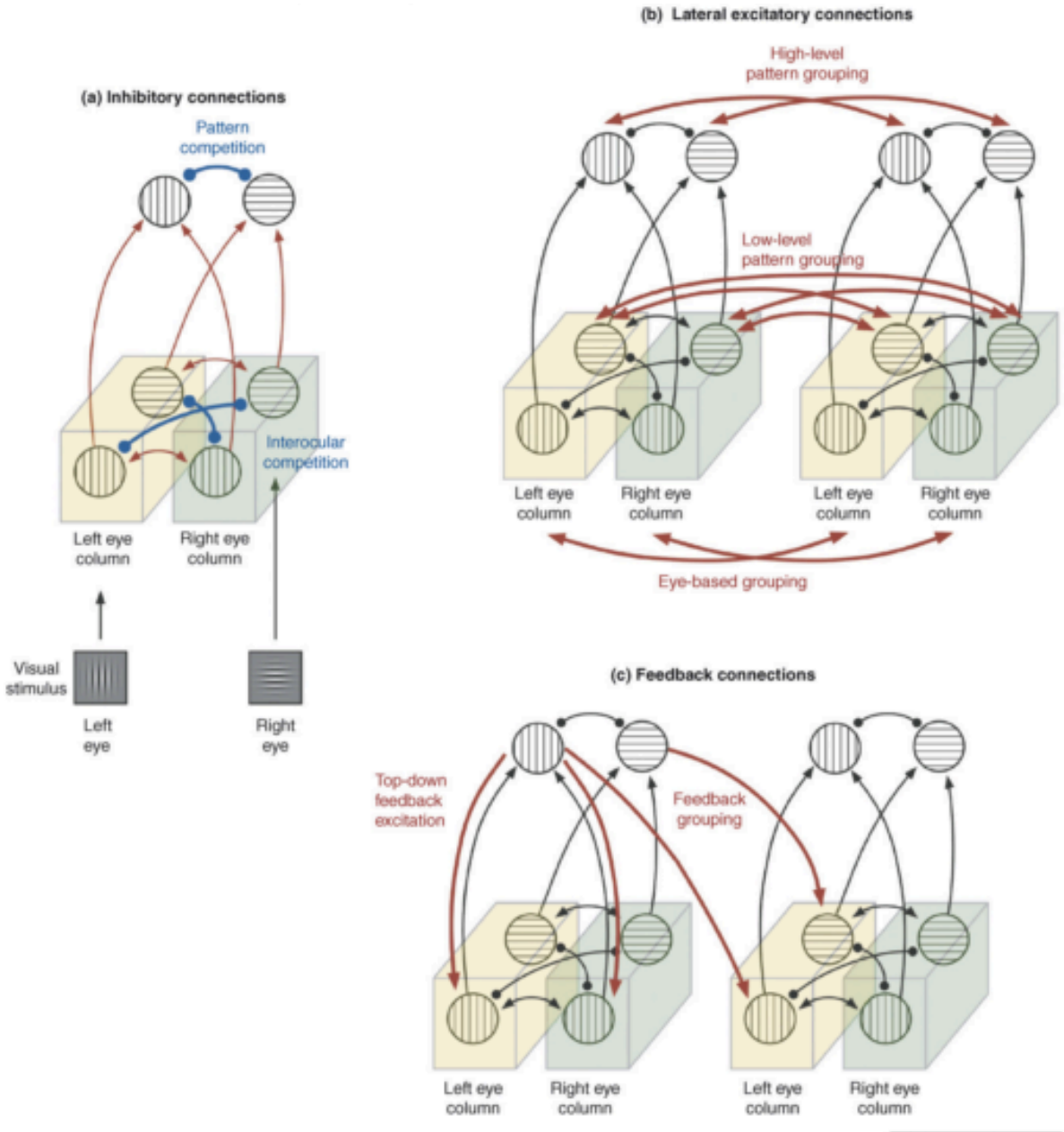


Figure 1.13: Hybrid binocular rivalry model. Lines with filled circles represents inhibitory whereas lines with arrows depict excitatory connections. (a) Blue lines with circles illustrate mutual inhibitory connections between monocular neurones and binocular neurones. (b) Red lines with arrows depict mutual excitatory connections. (c) Red lines with arrows show example a few possible excitatory feedback projections (Tong et al., 2006).

With the assumption that two populations of neurones compete during binocular rivalry (Figure 1.14A), two reasons for a 'trigger' of perceptual alternation were postulated. One

idea is that neural adaptation weakens the dominant stimulus over time and decreases its suppressive impact on the suppressed stimulus (Figure 1.14B) (e.g. Lehky, 1988; Mueller, 1990; Kalarickal and Marshall, 2000; Laing and Chow, 2002; Wilson, 2003; Lankheet, 2006; Blake, Tadin, Sobel, Raissian, and Chong, 2006; Seely and Chow, 2011). Laing and Chow (2002) suggested that spike frequency adaptation (reduction of cortical neurones firing rate frequency over time due to calcium-dependent potassium current (McCormick and Williamson, 1989; Huguenard and McCormick, 1992)) as well as synaptic depression (limitation of cortical neurones to respond to its inputs (Abbott, (1997)) generate perceptual alternation during binocular rivalry. Figure 1.14B depicts a model, which helps to understand the idea of self-adaptation. The black wavy line represents the state potential; the minima of each potential represent exclusive visibility (attractors). The black ball represents the actual system (perceptual) state, which moves between the two potential states. The state potential changes over time due to the adaptation of the current perceptual state and the simultaneous recovery of the suppressed state.

Another hypothesis, which tries to explain binocular rivalry alternation, is based on the assumption that random intrinsic noise within the visual system is the driving force for perceptual alternation (e.g. Brascamp et al., 2006; Kim et al., 2006; Rubén Moreno-Bote, Rinzel, and Rubin, 2007; Webber and Bressloff, 2013). The term ‘noise’ in this context means cortical processing variations such as vesicular (local neurotransmitter) release variations, spiking variations, and fluctuations in global neurotransmitter levels (Moreno-Bote et al., 2007). The potential state (Figure 1.14C) remains constant, but the intrinsic noise of the system, symbolised as dashed wavy arrow, drives the perception (black circle) into the other state potential. The adaptational force decreases with the reduction of the energy levels of the rival stimuli (e.g. luminance contrast) whereas the intrinsic noise remains little affected (Cao et al., 2016b). Moreover, the adaptation model implies a rapid change between the wells, but the existence of reversions and longer mixed periods argues against this idea as previously noted by Brascamp et al. (2006) who suggested intrinsic noise as an explanation for the results of binocular rivalry under low contrast stimulus conditions.

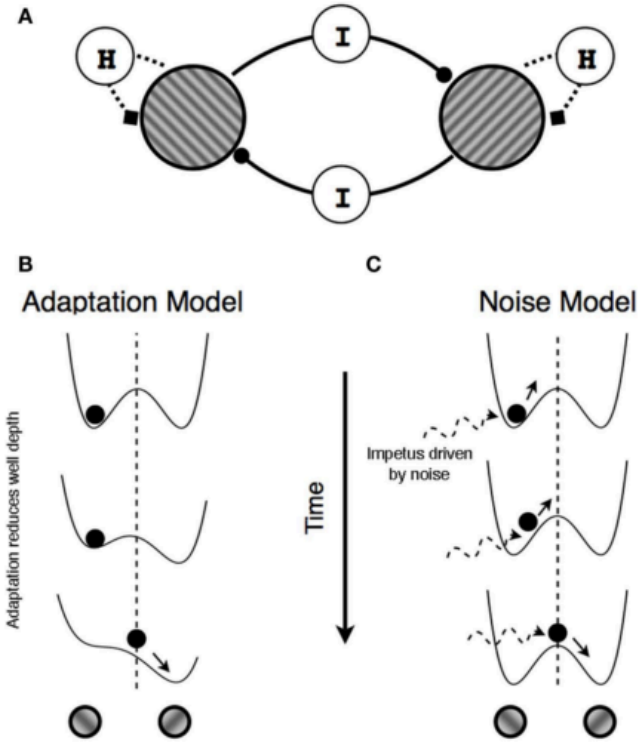


Figure 1.14: Models concerning the cause for alternation during binocular rivalry. A: Model of mutual inhibition. Neuronal projection of rival gratings (see bottom B and C), which inhibit each other (I) and at the same time, self-adapting (H). In B and C, energy landscape models are used to describe the continuous change of the perceptual states. The black ball depicts the perceptually dominant state, and the dashed line represents the transition zone (mixed perception). Whilst in the adaptation-based model (B) the perceptual change is caused by a change of well-depth due to adaptation, in the noise-based model, the well-depth is not affected, but instead, random noise impetus drives the perceptual alternation (Kang and Blake, 2011).

1.4.1.1 Alternative theory: Interhemispheric switches

In a series of publications, Pettigrew and collaborators suggested that competition in area V1 only cannot explain the various binocular rivalry findings (e.g. Pettigrew and Miller, 1998; Miller et al., 2000; Pettigrew, 2001; Carter and Pettigrew, 2003; Ngo, Liu, Tilley, Pettigrew, and Miller, 2008). Instead, the researchers suggested that binocular rivalry is a result of switches between the left and the right hemisphere involving various areas across the brain, mediated by an oscillator in the ventral tegmentum. This theory, however, was also criticised as it does not provide sufficient answers for instance on "…how a given hemisphere inherits a

particular monocular image during rivalry. “ (Blake and Logothetis, 2002, page 9). Also, it remains unclear how hemispheric switches could explain piecemeal and superimposed mixed states during binocular rivalry.

1.5 Stimulus characteristics and binocular rivalry

Since the very beginning of binocular rivalry investigations, researchers tried to understand the underlying reason for this perceptual alternation (Wheatstone, 1838; Hering, 1861; von Helmholtz, 1867). However, it was Breese who was the first to systematically investigate the effects of stimulus properties, such as size and blur, on the perceptual characteristics of binocular rivalry (Breese, 1899, 1909). In the following decades many scholars investigated the influence of different stimulus properties on binocular rivalry; these include contrast (e.g. Levelt, 1965; Liu et al., 1992; Bossink et al., 1993), size (e.g. Blake, O’Shea, and Mueller, 1992), spatial frequency (e.g. Kitterle and Thomas, 1980; O’Shea, Sims, and Govan, 1997; O’Shea, 1998), colour (e.g. Knapen, Kanai, Brascamp, van Boxtel, and van Ee, 2007), orientation (Wade, 1974; Schor, 1977), flicker (e.g O’Shea and Crassini, 1984), motion (e.g. Blake, Yu, Lokey, and Norman, 1998; Alais and Parker, 2012) and surrounding stimulus features (e.g. Takase, Yukumatsu, and Bingushi, 2013). All studies mentioned above used stimuli, which have been described as first-order or luminance-modulated. The following section will give an overview of the underlying processing mechanism for this stimulus type.

1.5.1 First-order stimuli

First-order, specifically luminance-modulated, stimuli can be differentiated from the background because of a change in luminance. Variations of luminance across the visual field, which correspond to specific receptive field properties of neurones in the visual cortex, for example, a luminance-defined grating (e.g. Campbell, Cooper, and Enroth-Cugell, 1969), will evoke responses from neurones that respond selectively to orientation and spatial frequency. These are so-called ‘simple cells’ (e.g. Hubel and Wiesel, 1962). The receptive fields of these simple cells have spatially segregated elongated sub-regions, alternating in excitatory and inhibitory effects (Figure 1.15A). As shown in Figure 1.15A, neurones with these corresponding receptive fields contain excitatory and inhibitory zones (Baker and Mareschal, 2001). A light bar presented in an excitatory zone will evoke a transient discharge

at its onset (On-response) and when a light bar is removed from an inhibitory zone (Off-response). Dark bars have the opposite effects (evoking On-responses from inhibitory zones and Off-responses from excitatory zones). Figure 1.15B depicts a scenario with an orientation difference between the grating stimulus and the excitatory and inhibitory zones, in which the excitatory and inhibitory influences cancel out. The opposite will happen when grating at the same orientation as the excitatory and inhibitory zones and will cause consistent stimulation of these sub-regions, which will synergistically sum to a strong response as shown in Figure 1.15C. However, if the light and dark regions of a grating correspond in orientation, but the excitatory and inhibitory zones contain both dark and light bars due to a higher spatial frequency, then the response will be weak (Figure 1.15D).

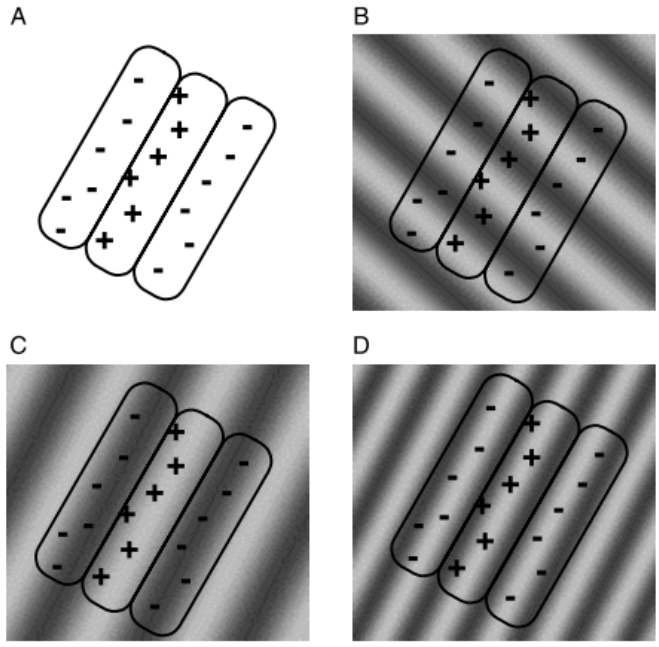


Figure 1.15: Scheme of spatial selectivity of cortical neurones for sinusoidal gratings (Baker and Mareschal, 2001).

Luminance-modulated stimuli are therefore differentiable from a background because of luminance variations across the space of that stimulus detected by simple cells in early visual cortex. However, the human visual system can also perceive stimuli, which do not show variations of their mean luminance, but of the contrast-modulation, which shall be the topic of the next section.

1.5.2 Second-order stimuli

There are in fact stimulus types that vary in contrast, texture, binocular disparity but with a mean luminance that is equal to the luminance of the background. Those stimuli are called second-order stimuli (e.g. Cavanagh and Mather, 1989). Second-order stimuli are suggested to be equivalent to higher-order signals from a natural environment (see review from Mareschal and Baker, 1999). The ability to locate and identify such second-order information can be explained by a model referred to as 'filter-rectify-filter', 'linear-nonlinear-linear' or 'second-order processing' (Graham and Landy, 2002). In the further course of this thesis, the term 'filter-rectify-filter' model will be used. As demonstrated in Figure 1.16, a linear spatiotemporal filter gives an orientation- and spatial-frequency-selective response to luminance. Then, the rectified output of the first filter is passed to a second linear filter that responds selectively to variations in the outputs of the first-order filters and represents this variation across regions of an image.

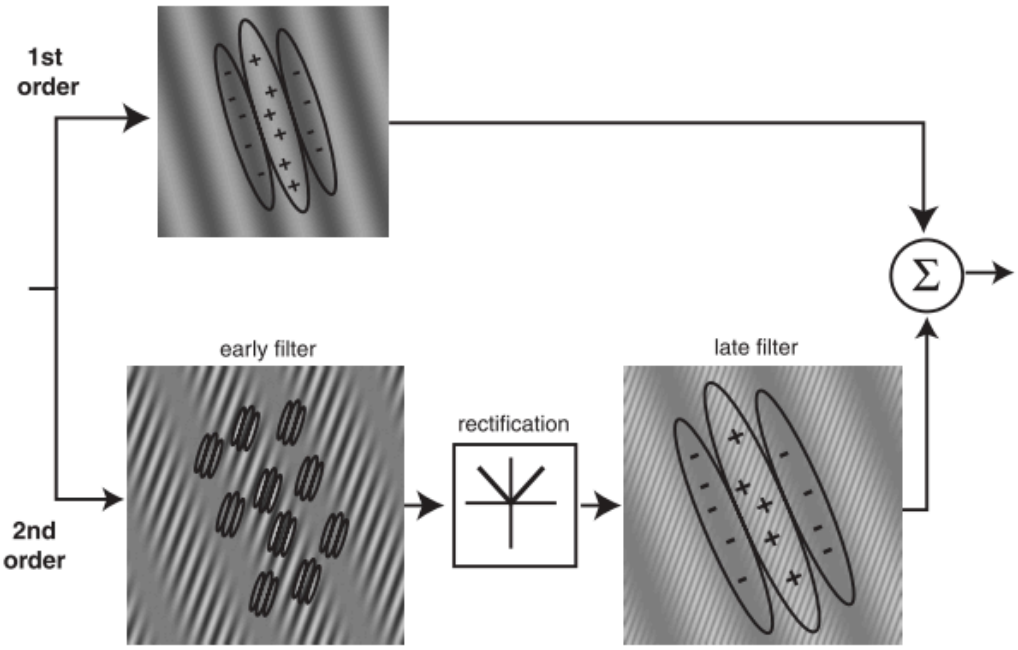


Figure 1.16: Model of first- and second-order stimuli processing. The top pathway demonstrates a luminance-defined, first-order stimulus processed by linear- spatiotemporal filters whereas the bottom pathway shows the filter-rectify-filter model for a second-order stimulus. The second-order stimulus shown, has a vertical, so-called 'carrier' with high-spatial frequency information and the so-called 'envelope' with low-spatial frequency (Baker and Mareschal, 2001).

The left side of the Figure 1.17 depicts a luminance-defined (L) grating (A) and a luminance-modulated (LM) grating with added binary two-dimensional visual noise (B). Both stimulus types are distinguishable from the background by luminance changes as shown in the luminance profiles (right side Figure 1.17A, B). A contrast-modulated (CM) grating has different local variations of luminance, i.e., different contrast, but the same mean luminance as the background (Figure 1.17C). The three different stimulus types, illustrated in Figure 1.17, can be mathematically described by the following equations (e.g. Schofield and Georgeson, 1999; Calvert et al., 2005).

Sinusoidal L grating:

$l_0(x,y) = l_0[1 + lsin(2\pi x f_x)]$

$l_0(x,y)$ is the luminance at position (x,y), l_0 is the mean luminance, l is the luminance modulation and f_x is the spatial frequency.

Sinusoidal LM grating:

$l_0(x,y) = l_0[1 + nN(x,y) + lsin(2\pi x f_x)]$

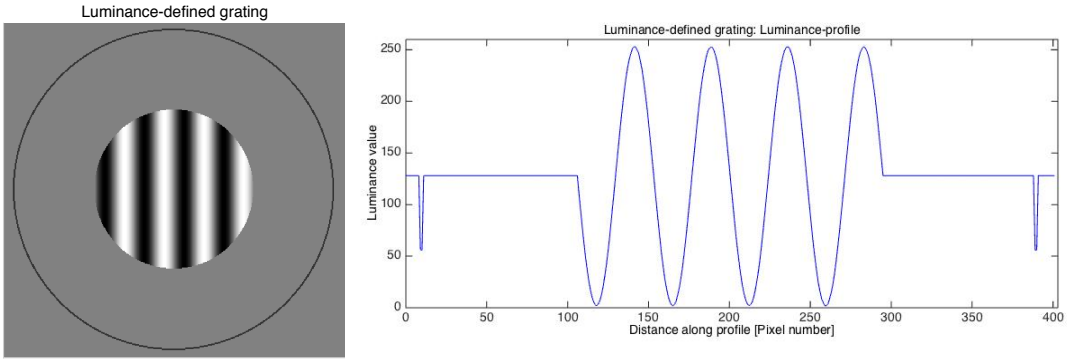
Two-dimensional binary white noise added to a vertical sinusoidal luminance grating. *N* is the binary noise at position (x,y) (either black (-1) or white (1)) and n is contrast of 0.2.

Sinusoidal CM grating:

$l_0(x,y) = l_0[1 + nN(x,y) + nN(x,y)msin(2\pi x f_x)]$

Contrast modulation is m. The mathematical term $nN(x,y)msin(2\pi x f_x)$ expresses the CM grating that results from the multiplying random noise sample by a sinusoid (Schofield and Georgeson, 1999; Calvert et al., 2005).

(A)



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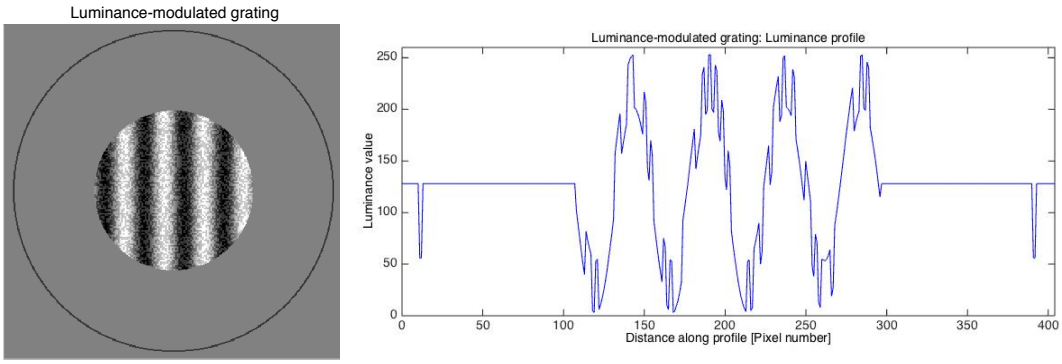

(C)

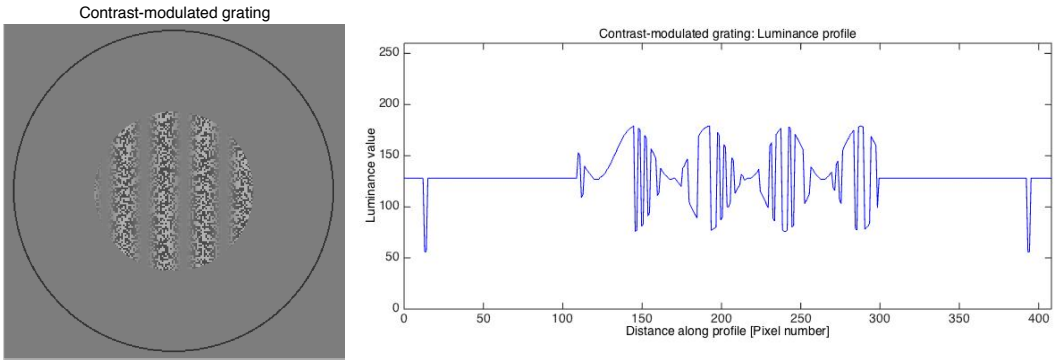

Figure 1.17: Illustration of vertical LM and CM gratings with luminance profiles for a horizontal line of pixels through the centre of the stimulus. (A) Luminance-defined sinusoidal grating with high contrast of 0.98. (B) LM sinusoidal grating with contrast of 0.78 and added two-dimensional binary noise with a contrast of 0.2. (C) CM sinusoidal grating with a two-dimensional binary noise carrier which had its contrast modulated by the grating (modulation of 1.0).

1.5.2.1 First-order input influence on second-order signals

Studying the visual perception of first but in particular second-order stimuli requires careful preparation of the stimulus conditions as well as calibration of the monitor to ensure that the intended signal is not confounded by any form of luminance artefact. In earlier investigations of second-order stimuli e.g. Victor and Conte, 1992; Ledgeway and Smith, 1994; Timothy Ledgeway and Smith, 1995, CM stimuli with carriers that contained static noise were used. However, images that use static noise have a locally unbalanced distribution of dark and light pixels. This local first-order artefact may confound the second-order signal and therefore static noise carriers are inappropriate for studying second-order characteristics (Smith and Ledgeway, 1997 and see also *Appendix*, Figure 1.17). Hence, dynamic noise carriers for CM stimuli (e.g. Schofield and Georgeson, 1999, 2000; Ellemberg, Allen, and Hess, 2004; Hairol and Waugh, 2010; Georgeson and Schofield, 2011; Zhou, Liu, Zhou, and Hess, 2014) are most suitable when investigating second-order spatial vision properties.

'Dynamic noise' refers to the alternation of dark and light noise checks, with a defined time course and usually randomly across a stimulus space to avoid any form of noise adaptation. The noise of two dichoptically presented stimuli can be either interocularly correlated (corresponding changes of noise checks in luminance, position and time), anti-correlated (corresponding changes of noise checks in position and time, but never in luminance) or uncorrelated (noise checks can be either correlated or anti-correlated). Both uncorrelated but particularly anti-correlated noise configurations have a potential to engage in rivalry competition as the interocular differences in luminance may generate mutual inhibition between the underlying neurones, processing the noise pages.

1.5.3 Neural locus of LM and CM stimuli

The psychophysical responses to LM and CM stimuli have been compared in a number of studies and the results of these studies suggested different processing mechanism for those stimulus types. Schofield and Georgeson (1999) measured contrast-sensitivity for L, LM and CM gratings. In one experiment, the participant had to detect LM or CM test gratings superimposed on weak LM and CM grating backgrounds. The results showed that LM background gratings facilitate the detection of LM test gratings, and CM background gratings also facilitate the detection of CM test gratings. However, only very slight or no facilitation

was found for the detection of LM gratings on a CM background whereas LM backgrounds did not facilitate the detection of CM test stimuli but they did mask detection. The result led the authors to the suggestion that CM and LM stimuli are detected by separate mechanisms.

Hairol, Formankiewicz, and Waugh (2013) measured visual acuity with LM and CM Landolt C stimuli. Although the stimuli were equated in visibility i.e. multiples of detection threshold, CM stimuli showed lower visual acuity than LM stimuli, which suggests the used processing sites with differently size properties for the two stimulus types.

Human cortical electric activity in the brain evoked with LM and CM dynamic binary noise gratings (Calvert et al., 2005) has also been investigated. Visual evoked potentials measurements were carried out whilst the participant gave responses to a psychophysical detection task for L, LM, and CM gratings. A significantly longer latency for CM gratings compared to LM gratings was found in the occipital area. Being in line with the 'filter-rectify-filter' model, the Calvert and co-workers speculated that the longer latency for second-order stimuli was due to additional processing in higher cortical areas for CM, than for LM stimuli. Larsson and collaborators presented first- and second-order texture defined grating stimuli and measured the metabolic activity in a wide range of lower and higher cortical visual areas (Larsson et al., 2006). Both LM and CM stimuli generate activity in various areas (V1, V2, V3, V3 A/B, and in the visual areas anterior to dorsal V3 called L01, hV4, and V01). Metabolic activity generated by LM stimuli was the same in extrastriate areas and V1 whereas CM stimuli generated larger activity in areas beyond V1.

Wong, Levi, and McGraw (2001) measured detection thresholds for LM and CM stimuli monocularly in individuals with amblyopia, and for the dominant eyes of healthy individuals. In almost all amblyopic, and in some preferred eyes of amblyopes, a relatively greater detection loss for CM, compared to LM stimuli was found. Visual sensitivity loss for amblyopic and preferred eyes in amblyopes to second-order information in particular, led Wong and collaborators to suggest that neurones involved are substantially more binocular, than those that process first-order information.

In a following study, Wong, Levi and McGraw (2005) investigated monocular detection thresholds for flanked and non-flanked CM stimuli in amblyopic and normal vision participants. The target stimulus was a horizontal CM grating, horizontally flanked with either

collinearly or orthogonally orientated CM gratings, which separation to the centre of target grating was varied between trials. The non-flanked results served as a baseline for both normal vision and amblyopic participants. Whilst flankers in normal vision participants facilitated CM detectability. On the other hand, the detection for amblyopic participants was impaired regardless, which eye was tested. The research group suggested therefore that the mechanisms, which mediate facilitatory and inhibitory effects, arise at or beyond neurones, which initially process binocular combination.

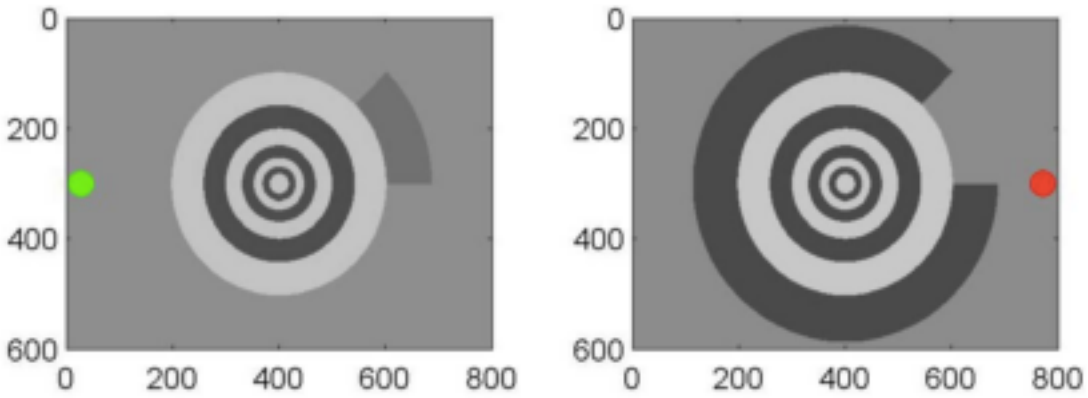

Figure 1.18: Example of L stimuli used in Chima et al.'s (2015, 2016) studies.

Chima, Formankiewicz and Waugh (2015, 2016) investigated interocular suppression, generated with either L, LM or CM stimuli. In one study, the research group disrupted binocularity by blurring one eye's vision (Chima, Formankiewicz, and Waugh, 2015), whilst in another study, binocularity was disrupted due to strabismus and microstrabismus. The participants had to fixate the centre of the ring stimuli (Figure 1.18) and simultaneously adjust the sector until it matched perceptually the surrounding ring, which then served as a measure of the depth of suppression. Use of CM rather than LM stimuli resulted in both studies in deeper measures of interocular suppression. Chima and co-workers suggested that CM envelope extraction and combination across the two eyes occurs at a later stage of visual processing than where binocular combination of the LM stimuli would first take place.

The studies listed in this section suggest different processing mechanisms for LM and CM stimuli. A study by Sukumar and Waugh (2007) suggested differently sized processing mechanisms of LM and CM stimuli. The researchers investigated spatial summation estimates at the fovea and at various eccentricities (up to 10 deg) for blob detection. Participants had to detect dynamic binary noise LM and CM Gaussian blobs of various sizes. Spatial summation areas for the processing of CM blobs were bigger than those of LM blobs at all eccentricities.

Sukumar and Waugh compared their results with findings from results from electrophysiological studies in primates and found that this differences between summation areas of LM and CM blobs were comparable with sizes of receptive fields in V1 and V2, even though the researchers did not rule out the possibility that CM processing could also arise within V1. The authors speculated that different summation areas for LM and CM blobs may be explained by a V2 site of second-order processing.

1.5.4 Second-order stimuli and binocular rivalry

The general aim of this review and the thesis on the whole is to investigate whether the proposed difference in processing sites of first- and second-order stimuli (e.g. Schofield and Georgeson, 1999; Wong et al., 2001; Hairol et al., 2013; Chima et al., 2015) is also reflected when first- and second-order stimuli are presented under binocular rivalry conditions. Prior to the author's publication on binocular rivalry and second-order stimuli (Skerswetat, Formankiewicz and Waugh, 2016), only two abstracts reported the results of investigations of binocular rivalry using second-order stimuli. Kim and collaborators reported that binocular rivalry for CM stimuli can be successfully generated using uncorrelated noise (Kim, Buckthought, and Wilson, 2006). In another abstract, Kim and collaborators (Kim, Kim, Chung, and Wilson, 2007) reported fMRI results during alternation under second-order conditions generated by uncorrelated dynamic carriers. No differences in V1 activity during phases of exclusive visibility could be found for both hemispheres whereas V2 showed fluctuation of activity during perceptual alternation. The authors suggested that V2 is specialised in the processing of second-order percepts. However, it remains unclear whether this alternation reported in both abstracts was due to the first-order input of the uncorrelated noise, the second-order component or maybe both.

1.6 Research Aims

Reviewing the literature on second-order spatial vision as well as on binocular rivalry has revealed gaps of knowledge, which this thesis aims to fill. The evidence presented above suggests that the initial site for processing CM stimuli lies further along the visual pathway than for L and LM stimuli. However, we know very little about the perception of CM stimuli under binocular rivalry conditions. An investigation of binocular rivalry characteristics for CM and LM stimuli will help to enhance the understanding of the underlying processing mechanisms of those stimulus types. In addition, the different processing sites that have been proposed for CM and LM stimuli might give rise to different characteristics of binocular rivalry for the two types of stimuli.

The experiments presented in this thesis have been formulated to answer the following questions:

Experiment 1: Investigations of binocular rivalry between luminance-modulated stimuli and between contrast-modulated stimuli under correlated noise conditions

Can orthogonally orientated and dichoptically presented CM gratings trigger perceptual alternation? If so, are the temporal characteristics of binocular rivalry generated by CM stimuli the same as for LM stimuli? It is known that an increase of stimulus size decreases the proportions of exclusive percepts for L stimuli (e.g. Breese., 1909; Blake et al., 1992; O'Shea et al., 1997) and also that binocular rivalry can occur in local zones throughout the percept (piecemeal state). It has also been suggested that mixed states involve, at least, partially binocular areas of the visual pathway (e.g. Liu, et al., 1992; Brascamp, van Ee, Noest, Jacobs, and van den Berg, 2006; Klink, Brascamp, Blake, and van Wezel, 2010). If mixed states are 'more binocular' then I can hypothesise that a higher proportion of mixed states for CM than for LM stimuli should occur because of the suggested more binocular site involved in the processing of CM than LM stimuli (e.g. Wong et al., 2001; Wong, Levi, and McGraw, 2005).

Experiment 2: The contribution of piecemeal and superimposed states to perception during binocular rivalry using luminance-modulated and contrast-modulated stimuli under anti-, un-, and correlated noise conditions

How does changing first-order input, by altering the inter-ocular noise correlation, change the course of binocular rivalry of LM and CM stimuli? Although, for CM stimuli, changing the interocular noise correlation does not affect stereopsis (Wilcox and Hess, 1996), binocular combination of contrast thresholds (Georgeson and Schofield, 2011) and binocular phase combination (Zhou et al., 2014, 2016; Zhou, Georgeson and Hess, 2014), un- and anti-correlated noise configurations provide different first-order input to the two eyes and could change the characteristics of rivalry (see Section *1.5.2.1 First-order input influence on second-order signals*).

Since results of studies have suggested that first-order stimuli are first processed in monocular stages (e.g. Hubel and Wiesel, 1959, 1962; Campbell and Kulikowski, 1966), it could be hypothesised that additional first-order input due to anti- and uncorrelated noise configurations should generate greater proportions of exclusive visibility and more perceptual alternations between the two exclusive states than correlated noise. Following this logic, the suggested binocular site of second-order stimuli would lead to fewer events of exclusive visibility and fewer alternations between the two exclusive states compared to those of first-order stimuli. This leads directly to the second question this experiment aims to answer: what are the contributions of the different mixed states, namely piecemeal perception and superimposition, to the overall perception during binocular rivalry? Whilst superimposition has been suggested as an indicator for binocular fusion (Liu et al., 1992, Brascamp et al., 2006; Burke et al., 1999) piecemeal perception is suggested to be rivalry in zones across the visual field (Blake et al., 1992). Hence, the testable hypothesis would be: CM stimuli generate fewer exclusively visible and piecemeal percepts, but engage in more superimposition, than do LM stimuli.

Experiment 3: Luminance-modulated stimuli in competition with contrast-modulated stimuli under binocular rivalry conditions

If CM and LM stimuli are processed by different spatial mechanisms, will this be reflected in competition between an LM and a CM stimulus under binocular rivalry conditions? Earlier in this section, it has been hypothesised that first-order input may drive exclusive visibility and alternation between exclusive states whereas second-order input has been thought to engage in superimposition. If true, then it is plausible to assume that when an LM stimulus is

presented to one eye and an orthogonally orientated CM stimulus to the other, greater proportions of exclusive visibility and more alternations would occur compared to results when only CM stimuli are used to initiate binocular rivalry. It remains to be seen whether LM or CM stimulus will predominate during binocular rivalry. As described earlier (see Section *1.2.1 Exclusive visibility, predominance, mean duration and alternation rate*), Levelt's laws suggest that variations in first-order stimulus strength have a significant influence on the perception during binocular rivalry (Levelt, 1965; Brascamp et al., 2015). Do these laws hold when LM stimuli with different visibility levels are in competition with a CM stimulus? If second-order stimuli are indeed processed in different areas compared to first-order stimuli, then Levelt's laws may not hold under these stimulus conditions.

Chapter 2 - Investigations of binocular rivalry between luminance-modulated stimuli and between contrast-modulated stimuli under correlated noise conditions

A modified version of this chapter has been published as:

Skerswetat, J., Formankiewicz, M.A. and Waugh, S.J., 2016. Very few exclusive percepts for contrast-modulated stimuli during binocular rivalry. *Vision research*, *121*, pp.10-22. [http://dx.doi.org/10.1016/j.visres.2016.01.002]

2.1 Introduction

Incompatible stimuli presented dichoptically can provoke competition between visual percepts, known as binocular rivalry (e.g. Wheatstone, 1838; Breese, 1899, 1909; Levelt, 1965). As a result of conflict during binocular rivalry, for a few seconds just one image will be perceived exclusively, whilst the other is suppressed. The dominance phases alternate between the two eyes over time. Different states of mixed percepts can also occur and can be categorized into piecemeal, when the perceived image, is made up of portions of each stimulus (e.g. Blake, 1989), superimposition in which both stimuli are perceived in their entirety, overlapping each other (e.g. Brascamp, van Ee, Noest, Jacobs, and van den Berg, 2006; and see also Liu, Tyler, and Schor, 1992), and transparency, where rival stimuli with very different spatial frequencies (Yang, Rose, and Blake, 1992) are seen at the same time, overlapping each other, but with one appearing in front of the other. When the interocular orientation difference between rivalrous gratings is small, mixed percepts appear to be "...inclined in depth" (Schor, 1977, page 587).

It has been suggested that competition between mainly monocular neurones is involved in the processing of exclusively visible percepts during traditional binocular rivalry (see review Tong, Meng, and Blake, 2006). In contrast, mixed states might represent the integration of two images at areas receiving predominantly binocular input along the visual pathway (Brascamp et al., 2006; Klink, Brascamp, Blake, and van Wezel, 2010; see also Liu et al., 1992).

Both early and later stages of the visual pathway are involved in binocular rivalry and sometimes stimulus rivalry overcomes binocular rivalry. For example, two rivalrous images shown to the two eyes, but with each containing parts of two stimuli, generate exclusive visibility of whole stimuli as a result of interocular grouping (Diaz-Caneja (1928) translated by Alais et al., 2000; Kovács et al., 1996), suggesting that binocular rivalry can lead to competition between percepts, rather than between eyes. Results of neuro-imaging studies also support the engagement of both low (Polonsky, Blake, Braun, and Heeger, 2000; Tong and Engel, 2001; Lee and Blake, 2002; Wunderlich, Schneider, and Kastner, 2005) and high visual areas (Tong, Nakayama, Vaughan, and Kanwisher, 1998; Buckthought, Jessula, and Mendola, 2011), as do results from a study using single-unit recordings from monkey (Leopold and Logothetis, 1996). Visual attention, a higher cortical process, also contributes

to binocular rivalry (for review, see Paffen and Alais, 2011) and eye movements might influence alternation of perception as saccades occur with high probability, just before an alternation during rivalry (van Dam and van Ee, 2006b). Nonetheless, results of traditional psychophysical studies have demonstrated that characteristics of binocular rivalry strongly depend on stimulus properties, such as contrast (Levelt, 1965; Bossink, Stalmeier and de Weert, 1993) and size (Breese, 1909; Blake, O'Shea, and Mueller, 1992; O'Shea, Sims, and Govan, 1997), which are first encoded at a low-level of the visual system.

Researchers of previous binocular rivalry investigations have predominantly used stimuli that contained elements differentiated from their background by luminance differences, called first-order or L stimuli, to initiate binocular rivalry alternation. The visual system is also capable of distinguishing between visual stimuli that differ from their background by changes in contrast, called second-order, or CM stimuli. CM stimuli can be constructed by modulating visual noise. To examine the effects of noise per se on stimulus processing, the same noise characteristics used to create CM stimuli, can be added to luminance-defined stimuli, to create LM stimuli. Both L and LM stimuli are in fact luminance-defined, but in this context, the luminance-defined stimuli modulate the noiseless background luminance, whereas luminance-modulated stimuli modulate the background that contains noise. The ability to locate and identify second-order information can be explained by a 'filter-rectify-filter' model (e.g. Mareschal and Baker, 1999; Landy and Graham, 2004 and see also Zhou and Baker, 1993). In this model, a linear spatiotemporal filter gives an orientation- and spatial frequency-selective response to luminance. Then, the rectified output of the first filter is passed to a second linear filter that responds selectively to variations in the outputs of the first-order filters and represents this variation across regions of an image.

Strong psychophysical evidence for separate mechanisms for the monocular processing of first- and second-order information was presented by Schofield and Georgeson (1999). The participant had to detect LM or CM test gratings superimposed on weak LM and CM grating backgrounds. The results showed that LM background gratings facilitate the detection of LM test gratings, and CM background gratings also facilitate the detection of CM test gratings. However, only very slight or no facilitation was found for the detection of LM gratings on a CM background, or vice versa.

Further support for different processing mechanism for first and second-order stimuli was provided from results of a fMRI study, in which the researchers presented first- and second-order texture defined grating stimuli and measured the metabolic activity in a wide range of lower and higher cortical visual areas (Larsson, Landy and Heeger, 2006). Both first- and second-order stimuli generate activity in various areas (V1, V2, V3, V3 A/B, and in the visual areas anterior to dorsal V3 called L01, hV4, and V01). Whilst for first-order stimuli the activity in extrastriate areas was the same as in V1, second-order stimuli generated larger activity in areas beyond V1 (e.g. V01).

Calvert and co-workers (Calvert et al., 2005) measured VEPs as the participant gave responses to a psychophysical detection task for L, LM and CM gratings. A significantly longer latency for CM gratings compared to LM gratings was found in the occipital area. The authors proposed that the longer latency for second-order stimuli was due to additional processing that involves higher cortical areas for CM, than for LM stimuli.

The involvement of areas receiving predominantly binocular input, i.e. beyond the entry level of V1, in the visual processing of CM stimuli was also suggested by Wong, Levi, and McGraw (2001). Detection thresholds for LM and CM stimuli were measured monocularly in individuals with amblyopia and for the dominant eyes of healthy individuals. Amblyopia is a neural disorder characterised by presence of strabismus, anisometropia, or a form of deprivation (e.g. congenital cataract or corneal haziness). It is associated with reduced spatial visual performance, e.g. acuity, but also disruption of binocular function, e.g. stereopsis. In almost all amblyopic and in some preferred eyes of amblyopes, a relatively greater detection loss for CM, compared to LM stimuli was found. Visual sensitivity loss for amblyopic and preferred eyes in amblyopes to second-order information, in particular, led Wong and collaborators to suggest that neurones involved are substantially more binocular, than those that process first-order information.

In a recent study of interocular blur suppression of first- and second-order stimuli by Chima, Formankiewicz, and Waugh (2015), binocularity of the visual system was disturbed by blurring one eye. Use of CM rather than LM stimuli resulted in deeper measures of interocular suppression. This suggests that CM envelope extraction and combination across the two eyes occurs at a later stage of visual processing than where binocular combination of the LM stimuli would first take place.

The evidence presented above suggests that the initial site for processing of CM stimuli lies further along the visual pathway than for LM stimuli. However, we know very little about the perception of CM stimuli under binocular rivalry conditions. An investigation of CM perception during binocular rivalry will help to enhance the understanding of the processing mechanisms of CM stimuli in the early visual cortex. In addition, the different processing sites that have been proposed for CM and LM stimuli might give rise to different characteristics of binocular rivalry for the two types of stimuli.

2.2 Methods

The following section will describe the general methodology used for all experiments in this thesis. Deviations from the methods described in this section or additional aspects will be addressed separately in each experimental chapter.

2.2.1 Observers

Six male and five female participants with an average age of 25.8 (± 5.4 (standard deviation)) years completed the study. One participant was excluded because of ongoing lack of concentration during the experimental task. Four of the ten remaining participants were experienced observers in binocular rivalry experiments (including one of the authors, J.S.) whilst the other six were inexperienced psychophysical observers. All observers except author J.S. were unaware of the purpose of the study. All observers had normal or corrected-to-normal vision with visual acuity of at least 6/6 and normal binocular vision as indicated by random-dot-stereopsis of at least 60 arcsec when measured with the Dutch Organization for Applied Scientific Research (TNO) stereo test (Lameris Ootech, Ede, Netherlands).

2.2.2 Stimuli

For all three stimulus types, horizontal and vertical sinusoidal gratings in circular windows, and sizes of 1, 2, 4 deg containing spatial frequencies of 4, 2, 1 c/deg, respectively, were used. The sizes and spatial frequencies of the gratings were co-varied to maintain a constant

bandwidth for all stimuli. LM gratings were created by adding dynamic binary noise with an amplitude of 0.2 to the sine wave. The same noise amplitude was multiplied by the sine wave to create the CM gratings. For each stimulus type, close to maximum producible modulation was used, i.e. 1.0 for CM, 0.78 for LM and 0.98 for L stimuli (see Section *1.5.2 Second-order stimuli*). The stimuli were presented on a grey background with a mean luminance of 60.5 cd/m^2. The effective viewing distance was 100 cm and the screen pixel size at this distance was 1.3 arcmin.

The stimuli were presented dichoptically, such that the right eye saw the horizontal grating and the left eye, the vertical grating. A fusion lock seen by both eyes, here a surrounding annulus, was used to aid fusion and had a width of 2.6 arcmin or 2 pixels and its diameter was twice that of the grating (Figure 1.16). Dynamic noise carriers are useful for the creation of CM stimuli (e.g. Schofield and Georgeson, 2000; Hairol and Waugh, 2010; Georgeson and Schofield, 2011; Zhou, Liu, Zhou, and Hess, 2014) since static noise carriers can result in clusters of first-order artefacts (Smith and Ledgeway, 1997). Therefore, in the current study, dynamic noise carriers were created by random presentation of ten stimulus pages, which were created using the equations described above with randomly generated noise patterns. The noise patterns were always the same in the two eyes, i.e. correlated. The noise check size was 2 x 2 pixels and each noise page was displayed for 14.28ms (2 monitor frames with the monitor running at 140 Hz).

2.2.3 Apparatus and calibration

A Dell Precision 3500 with an operating system of Microsoft Windows XP Professional (Version 2002) was used to run the experiment and store the data. Stimuli were generated using the Cambridge Research Systems Visual Stimulus Generator, which was run by a custom written Matlab program (Version R2010b). A Mitsubishi Diamond Pro 2070SB CRT Monitor (with a resolution of 1027 x 769 pixel) was used for presenting the stimuli. Gamma correction was carried out periodically using the Cambridge Research Systems ColorCal and software to produce lookup tables and ensure the output of the intended luminance. Before each experiment began, the monitor was warmed up for 30 minutes to achieve consistency of mean luminance.

It is important to ensure that second-order stimuli do not contain first-order artefacts. The use of dynamic noise (as described above) helps to eliminate luminance clumping. However, adjacent pixel non-linearity (APNL) (Klein, Hu and Carney, 1996), which occurs when luminance levels of adjacent pixels cannot be reliably created, can lead to variation of local mean luminance. Manahilov and collaborators (Manahilov, Calvert and Simpson, 2003) reported that dynamic noise of at least 2 x 2 pixels does not give rise to APNL artefacts. Our stimuli satisfied this criterion. We also made photometric measurements of our stimuli. The mean luminance of CM vertical and horizontal gratings did not vary with a change in contrast confirming that these did not contain luminance artefacts (see Appendix *6.1 Stimulus calibration*).

A four mirror stereoscope composed of optical components by OptoSigma (OptoSigma Corporation, California, USA) was used to present a horizontal grating to the right eye and a vertical grating to the left eye. The mirrors were carefully aligned prior to beginning the experiments to ensure that only one stimulus was visible to each eye.

2.2.4 Procedure

The experiment followed the ethical procedures of the Helsinki declaration of 1975. All participants gave informed consent and were reimbursed for time spent. The experiment was approved by the appropriate Anglia Ruskin University Ethics Committee (FST/FREP/12/327).

All experiments were performed in a dark room. Participants sat on a comfortable chair and placed their heads in a chinrest. Before the actual experiment was initiated, the stimuli were aligned for each individual by adjusting the position of a left and right nonious marker on the screen. This was done to ensure comfortable viewing with both eyes during the experiment.

The participant's task was to press and hold the left button on a response box when only the vertical grating (left eye image) was visible, or the right button when only the horizontal grating (right eye image) was visible. If the percepts began to intermingle with each other or if the two percepts were superimposed, the participants were instructed to press and hold both buttons. No button presses indicated invalid responses. Participants were permitted to view any part of the image patch throughout the trial.

Blocks of L, LM or CM stimuli in different order of sizes were presented in a counterbalanced order. One trial lasted at least 120 s. Each stimulus condition was repeated 8 times. Instructions and practice trials were given before the data collection of the main experiment started. Breaks in-between trials were permitted if needed. A long break after half of the trials in a session were completed was enforced. Therefore, one full session lasted between 60 and 90 minutes, depending on the breaks for each individual. Four sessions were carried out on separate days for each participant.

2.2.5 Data analysis

During each trial, a key or key combination was pressed and held as long as the participant perceived the actual perceptual state. This was recorded and stored in data files. Then, the number of perceptual changes, total duration of visual exclusivity (sum of horizontal (H) and vertical (V) percepts) as well as mixed (M) percepts were calculated across 120 s. The mean duration of each percept was also analysed. The last perceptual response of a trial was not included in these calculations, as its duration would have been reduced by the termination of the trial at 120 s. When a percept did not occur during a trial (e.g. the observer never reported a vertical grating), a duration of 0 s was used in calculating the mean across trials to reflect the absence of a certain percept.

Binocular rivalry is often described as an ongoing perceptual change between two rival stimuli. In fact, that is not entirely true. The following perceptual changes were therefore also analysed (Figure 2.1). Full flips are changes from one exclusive percept to another (button presses from H to V or V to H) without a mixed percept in-between. Half flips are perceptual changes that occur from an exclusive to a mixed percept, and vice versa (H to M, M to H, V to M, M to V). Reversions represent a change from one exclusive percept to a mixed one and back again to the same exclusive percept (e.g. Mueller and Blake, 1989; Robertson, Kravitz, Freyberg, Baron-Cohen, and Baker, 2013) (button presses from H to M to H or from V to M to V).

If one exclusively visible percept followed on directly after the other (i.e. a vertical grating was seen and then a horizontal one, or vice versa as indicated by a change in pressing button from V to H or H to V), an invalid or mixed response may have occurred because of the

possibility that for a short time either no button (invalid response) or both buttons (mixed response) were pressed. Also, inaccurate button pressings may confound the data with extremely short responses during a trial. Hence, a reaction time control experiment was carried out to extract these unwanted responses in the following way. Vertical and horizontal CM gratings with a size of 1 deg and spatial frequency of 4 c/deg were presented monocularly through the stereoscope. The vertical grating was presented to the left eye for a specific amount of time and then the horizontal grating was presented to the right eye. Each presentation lasted for a duration that was picked from a normal distribution with a mean of 3 s and a standard deviation of 1 s. In a trial, the presentation of horizontal and vertical grating alternated and each grating was presented 20 times. Four participants were instructed to indicate the physical changes of the percept with the same button presses as were used for the main experiment. After extracting the duration of invalid and mixed responses during these real 'full' perceptual changes, the mean and standard deviation for each participant was calculated. The mean summed with two standard deviations was calculated individually and was finally averaged across participants to serve as a threshold. Based on the results of this control experiment, all perceptual durations $\leq$ 180 ms were excluded from the data analysis.

2.2.5.1 Statistical analysis

A customized Matlab program was used to analyse the raw data generated from this study. The final data were analysed using Statistica (Stat Soft, Int., U.S.A.), in which a repeated measure ANOVA with Greenhouse-Geisser correction was carried out. For *post-hoc* pairwise comparisons, a Bonferroni correction was used. Planned comparisons were also carried out to analyse interactions between various levels.

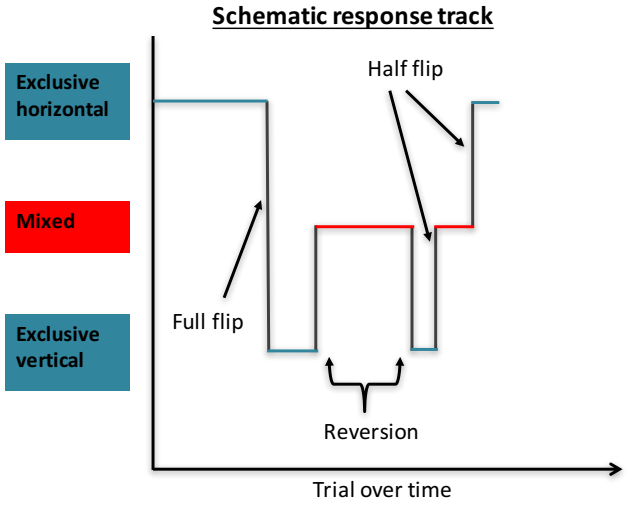

Figure 2.1: Illustration of a response track and the perceptual changes that were analysed in this experiment.

2.4 Results: Effect of stimulus type and size

Figure 2.2A shows exclusive visibility, i.e. the proportion of time during which either the horizontal or vertical gratings only were perceived for the three stimulus sizes and types used in the experiment, averaged across participants. In this section, I refer to stimulus size, but since size and spatial frequency co-varied, the reported effects of size, could also represent effects of spatial frequency. Averaged across size, exclusive visibility was 56.7 ± 5.43 (standard error), 57.3 ± 5.40, 14.6 ± 4.48%, for L, LM and CM stimuli, respectively. A statistical analysis using a repeated measure ANOVA of the effects of stimulus type (L, LM, and CM) and size (1, 2 and 4 deg) on exclusive visibility was carried out. A very highly significant main effect of type was found [$F(1.09, 9.85) = 69.73$, $p < 0.001$]. *Post-hoc* analysis indicated that there was no significant difference in exclusive visibility between L and LM stimuli [$p > 0.05$] whereas CM stimuli produced significantly less exclusive visibility than L and LM stimuli [$p < 0.001$]. A significant effect of stimulus size on exclusive visibility could also be demonstrated [$F(1.62, 14.54) = 23.35$, $p < 0.001$]. All three sizes were significantly different from each other [post-hoc, $p < 0.05$] with a reduction in exclusive visibility as the stimulus size increased.

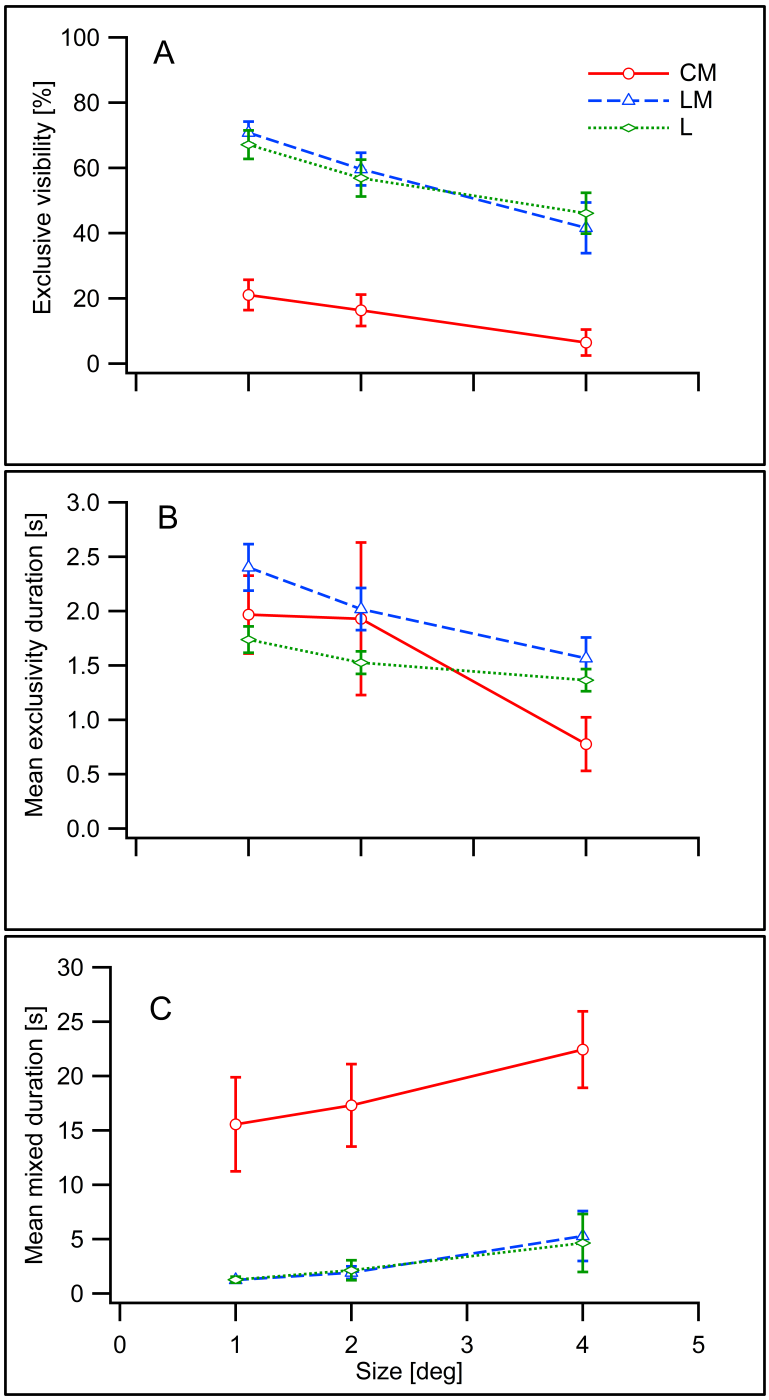

Figure 2.2: Average of all participants' (A) exclusive visibility, (B) dominance duration, and (C) mixed duration for three sizes of L (diamond symbols, dotted lines), LM (triangle symbols, dashed lines) and CM stimuli (circle symbols, solid lines). Vertical bars represent ±1 standard error.

Exclusive visibility represents the proportion of time in a trial during which responses indicate perception based on the right-eye only, or on the left-eye only. When the percept is not exclusive, it is mixed. The proportion of time during which mixed perception in a trial

occurs is higher for CM than LM stimuli. Both of these (i.e. relative proportion of exclusive and mixed perceptions) take into account the mean duration of each percept and their frequency.

Mean exclusivity and mixed durations are shown in Figure 2.2B and Figure 2.2C, respectively. The statistical significance of the effects of stimulus size and type was assessed in separate ANOVAs for exclusivity and for mixed duration. Averaged across size, mean exclusivity duration was 1.54 ± 0.11, 2.00 ± 0.20, 1.56 ± 0.44 s, for L, LM and CM stimuli, respectively. Exclusivity duration reduced with an increase in stimulus size for all types of stimuli [$F(1.75, 15.75) = 12.85$, $p < 0.001$] and was not affected by stimulus type [$F(1.10, 9.90) = 1.50$, $p > 0.05$]. Averaged across size, mean mixed duration was 2.68 ± 1.29, 2.82 ± 1.01, 18.44 ± 3.88 s, for L, LM and CM stimuli, respectively. Mixed duration increased with an increase in size [$F(1.69, 15.17) = 8.72$, $p < 0.01$] and was also affected significantly by stimulus type [$F(1.03, 9.23) = 34.96$, $p < 0.001$], being longer for CM than LM and L stimuli [post-hoc, $p < 0.01$].

More perceptual changes were also observed for L and LM stimuli, than for CM stimuli (Figure 2.3). The full flip rate (a perceptual change between two exclusive percepts without a mixed percept in-between) averaged across participants and stimuli size was 8.6 ± 2.5, 5.8 ± 1.6 and 0.3 ± 0.1 flips/120 s trial for L, LM, and CM stimuli, respectively. There were more half flips (perceptual change from an exclusive to a mixed percept, and vice versa) than full flips in a trial. L and LM stimuli produced more half flips than CM stimuli (L: 64.5 ± 7.3, LM: 54.4 ± 6.3, CM: 14.9 ± 5.2). An analysis of the reversion rate (perceptual change from an exclusive percept to a mixed one and back again to the same exclusive percept) showed again a similar pattern, however, the number of reversions for L (6.9 ± 1.2) and LM (6.0 ± 0.9) was only twice that for CM (3.5 ± 1.2) stimuli.

The statistical significance of the effects of stimulus type and size were assessed in a separate repeated-measures ANOVA for each type of perceptual change.

An interaction between size and stimulus type for full flips could be shown [$F(1.55, 13.98) = 6.92$, $p < 0.05$]. A planned comparison showed that L stimuli varied throughout all sizes [$p < 0.05$] and LM stimuli varied between 2 and 4 deg stimuli sizes [$p < 0.05$], but not between 1 and 2 deg [$p > 0.05$]. In contrast to that, full flips occurred very rarely for CM stimuli and

were not affected by changes in stimulus size [planned comparison, $p > 0.05$]. The numbers of full flips were significantly different between all types of stimuli [$p < 0.05$].

The analysis of half flips revealed a main effect for the type [$F(1.08, 9.73) = 40.73$, $p < 0.001$], but not for the size [$p > 0.05$]. All types differed significantly from each other [post-hoc, $p < 0.05$].

For reversions, an interaction between stimulus type and size [$F(2.58, 23.24) = 4.08$, $p < 0.05$] was found. The number of CM reversions was significantly different from the numbers of L [$p < 0.05$]; and almost significantly different from the number of LM reversions [$p = 0.05$]. The effect of size was significant only for CM stimuli [$p < 0.05$].

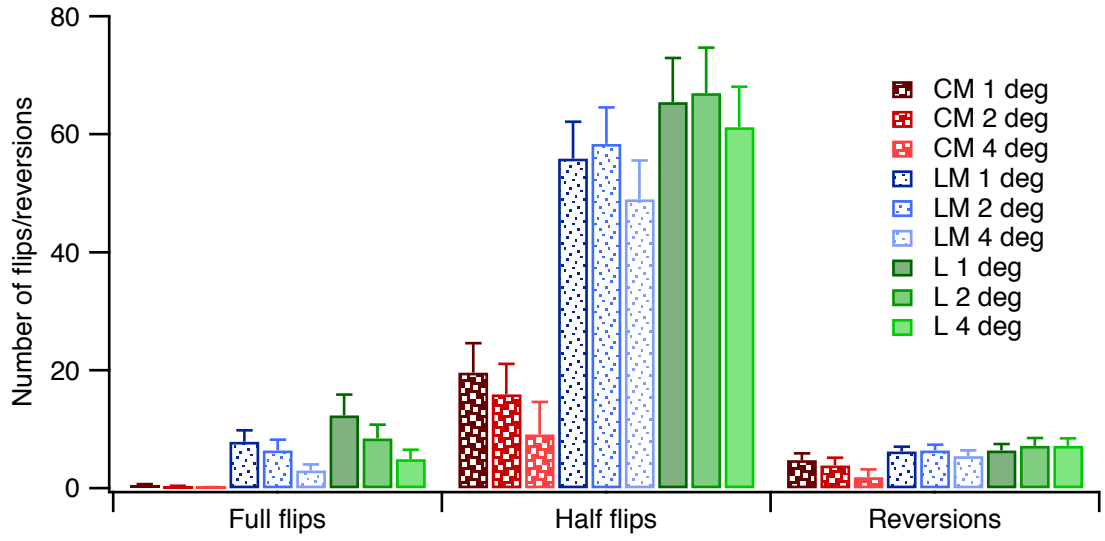

Figure 2.3: Number of full flips, half flips, and reversions for L (green, solid bars), LM (blue, bars with small dots), and CM (red, bars with big dots) stimuli, averaged across participants. The different hues of the specific stimulus types represent the various stimuli sizes (dark 1 deg, medium 2 deg, light 4 deg). Vertical bars represent +1 standard error.

2.5 Control experiment: effect of visibility levels

After I demonstrated that CM stimuli show significantly lower proportions of exclusive visibility and a lower rate of full, half flips, and reversions than L and LM stimuli, it was necessary to determine whether the differences between the results are due to the differences in perceived visibility of the L, LM, and CM gratings. This is a possibility because it is known that the alternation rate increases with an increase in visibility level or contrast for L stimuli (Levelt, 1965; Brascamp, Klink, and Levelt, 2015).

2.5.1 Methods

Detection threshold measurement: Detection thresholds for LM and CM stimuli were measured using a method of constant stimuli. Stimuli with a size of 2 deg and a spatial frequency of 2 c/deg, and the same noise characteristics as in the main experiment, were used. A two-alternative temporal forced choice task in which participants had to indicate whether the first or second interval contained the grating was used. Dichoptic presentation was achieved with a stereoscope (as in the first experiment) but only one stimulus was presented briefly (500 ms) to one eye whilst the other eye saw a mean luminance screen. The time interval from one presentation to the next was 500 ms. Eleven contrast levels were used separated by 1.5 dB (0.075 log) steps. These were chosen to span the full psychometric function for each condition and participant, i.e. from guess rate (50%) to 100% correct responses. Five participants from the first experiment of this chapter took part in this experiment. 125 trials were presented in each run and four runs were performed. A baseline contrast value for each eye was determined in short run using 70 trials.

Binocular rivalry using four different modulation levels for LM stimuli: LM stimuli were presented using four different modulations (0.78, 0.40, 0.20 and 0.10) and were compared with CM results of the main experiment of this chapter (modulation 1.0). Stimulus size was 2 deg diameter containing a 2 c/deg spatial frequency. Noise conditions and the experimental procedures were the same as in the main experiment. Thirty two trials (4 modulations x 8 repeats) in a counterbalanced order were carried out in two sessions; one session per day.

2.5.2 Data analysis

Detection threshold measurement: Performance data for the 11 different contrast levels were calculated for each condition and participant. These data were fit with a Weibull function using Igor Pro software to obtain contrast threshold for 75% correct performance, the slope of the function and the chi-square. The function fits were weighted by the inverse standard errors. The mathematical expression for the Weibull formula is:

$$P_{correct}(c) = 1 - 0.5 * 2^{-(c/th)^{\beta}}$$

c is the target contrast*, th* is the estimated threshold at 75% correct response and β is the slope of the function (Yu, Klein, and Levi, 2002; Hairol and Waugh, 2010).

Binocular rivalry using 4 different modulation levels for LM stimuli: Data analysis followed the analysis of the main experiment. In addition, exclusive visibility over trial time was also calculated as follows. A trial was separated into 3-s bins. The sum of exclusive and mixed percepts provided the total perceptual time (invalid responses were excluded). Then, the relative amounts of exclusive and mixed percepts were calculated for every 3-s interval, which provided a sufficiently fine time scale to show changes over time, (i.e. the mean exclusivity duration averaged across stimuli type, contrast level and participants was 2.2 s). The averages across trials were calculated for each individual and these were then averaged across participants.

Since the individual detection thresholds for LM and CM stimuli were known, it was possible to determine and compare visibility of LM and CM gratings. The visibility was calculated by dividing the modulation level used in the current experiment by the detection threshold of each eye. Right and left visibilities were then averaged to a visibility for each individual. Finally, visibilities were averaged across participants to get an average visibility value for LM and CM stimuli. Therefore, within each set of experiments, all individuals ran the experiment at the same modulation level (as specified) and not at modulation levels based on the individual thresholds. The intention was to generate baseline visibility levels and estimates of their variations across participants. The variation (standard error) across participants ranged from 15% - 17% and this would have not influenced the interpretation of our results.

2.5.3 Results

For the modulation used in the main experiment, visibilities averaged across participants and both eyes were 7x ± 0.96 (standard error) for CM stimuli (modulation of 1.0) and 43x ± 6.49 for LM stimuli (modulation of 0.78). For the LM stimuli used in the control experiment, visibilities were 22x ± 3.33 for modulation of 0.40, 11x ± 1.66 for modulation of 0.20, and 5x ± 0.83 for modulation of 0.10. A similar level of visibility for LM and CM stimuli is therefore achieved when the luminance modulation is 0.1 (and CM modulation is 1.0).

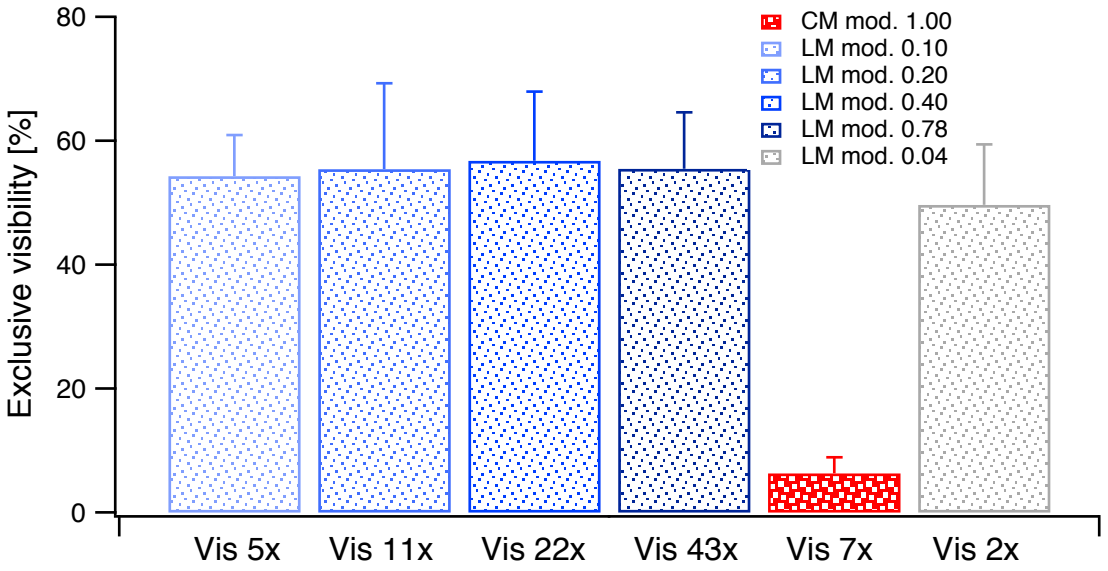

Figure 2.4: Exclusive visibility, in percent, for different LM (blue, bars with small dots) and CM (red, bars with big dots) stimuli. The blue hues represent the different modulation levels (shown in the legend) and therefore the different visibilities (Vis) (multiples over detection threshold, for example Vis 5x refers to an averaged visibility level of 5 times above detection threshold). The grey bar with small dots on the right side of the graph represents results averaged for 2 participants for LM stimuli presented near detection threshold. Vertical bars represent +1 standard error.

In this section, statistical analyses were performed firstly to investigate the effects of luminance modulation (or visibility as multiples of detection threshold) on characteristics of binocular rivalry. To compare the characteristics for LM and CM stimuli, a separate ANOVA was carried using the data generated by stimuli with similar levels over the detection threshold, i.e. a modulation of 0.1 for LM and 1.0 for CM.

The exclusive visibility for the LM stimuli (Figure 2.4) are stable regardless of the modulation [$F(1.35, 5.39)= 0.07$, $p > 0.05$]. CM stimuli generated a significantly lower proportion of exclusively visible percepts (10.1 ±4.15 %) than LM stimuli (53.5 ± 6.35 %) when both were presented at similar multiples of detection threshold [$F(1, 4)= 29.65$, $p < 0.01$]. In a subsequent control experiment on 2 participants, it was found that even near detection threshold (approximately 2x above), LM stimuli generate more exclusively visible percepts than CM stimuli (see grey bar in Figure 2.4 and Section *2.7.2 Effect of visibility levels on binocular rivalry*).

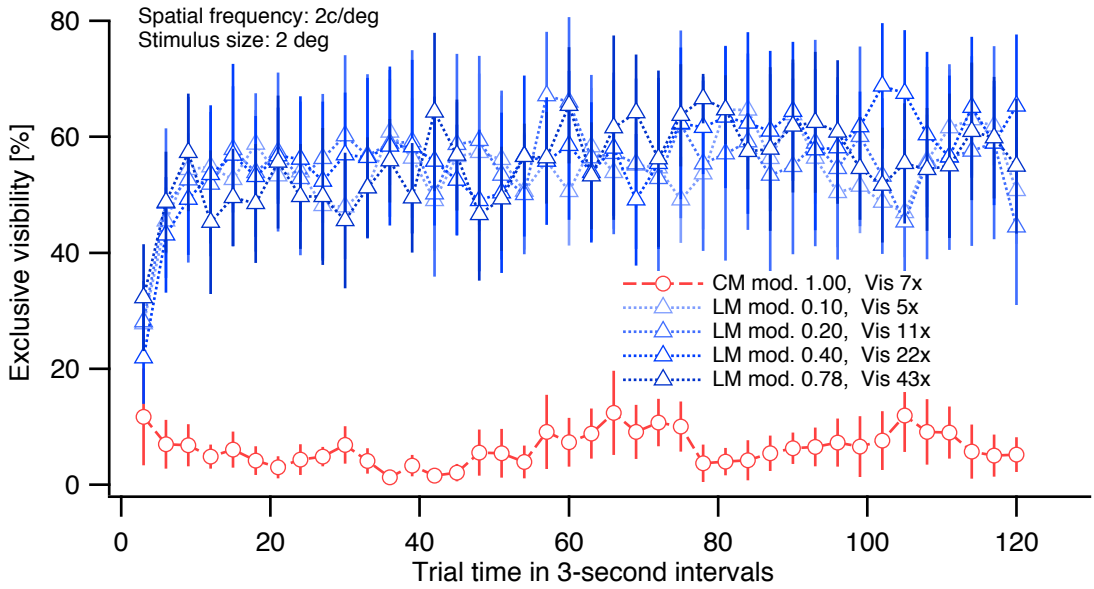

Figure 2.5: Average exclusive visibility for all participants in percent calculated every 3 s over 120 s in total. The various blue, dotted functions represent the LM stimuli (triangle symbols) with luminance contrast of 0.10, 0.20, 0.40 and 0.78. CM stimulus (circle symbol) is plotted in red with a dashed line. The visibilities for the different stimuli are depicted in the legend. Vertical bars represent ±1 standard error.

Figure 2.5 shows exclusive visibility analysed across the trial time, in 3-s intervals. An unambiguous difference in exclusive visibility over time is observed between LM and CM stimuli: exclusive visibility is always lower for CM than LM stimuli.

Statistical analysis of exclusive visibility over 120 s for LM stimuli could not demonstrate any significant effects of contrast [$F(1.30, 5.18)= 0.04$, $p > 0.05$] or time [$F(2.63, 10.53)=3.17$, $p > 0.05$]. Exclusive visibility for CM stimuli also did not show a significant change over 120 s [$F(2.20, 8.80)= 0.80$, $p > 0.05$]. Small effects between single '3-s-bins' might be not revealed

with an ANOVA that analyses across forty '3-s-bins'. Therefore, I also planned comparisons to analyse differences between single '3-s-bins'. A planned comparison was carried out to compare exclusive visibility over the first seconds after initiating binocular rivalry. A comparison of all LM stimuli with different contrast levels showed that exclusive visibility increases significantly between the first '3-s bin' and the second '3-s bin' [$F(1, 4)=9.66$, $p < 0.05$] but no further significant increase between the second and third '3 s bin' [$p > 0.05$]. CM stimuli on the contrary showed no significant change over the first 9 s (i.e. the first three 3-s bins) [$p > 0.05$].

Numbers of full flips, half flips and reversions are plotted in Figure 2.6. The increase in modulation (and visibility) for LM stimuli significantly increased the number of full flips [$F(1.81, 7.25)= 4.87$, $p < 0.05$] and half-flips [$F(1.67, 6.70)= 11.36$, $p < 0.01$]. The number of reversions was not affected by changing the LM visibility [$F(1.77, 7.08)= 0.84$, $p > 0.05$]. A statistical comparison of the number of perceptual changes for similarly visible LM and CM stimuli (LM with a modulation of 0.1 and the CM with a modulation of 1.0) showed significantly fewer full flips [$F(1, 4)= 11.03$, $p < 0.05$], half flips [$F(1, 4)= 28.93$, $p < 0.01$], and reversions [$F(1, 4)= 37.45$, $p < 0.01$] for CM compared to LM stimuli.

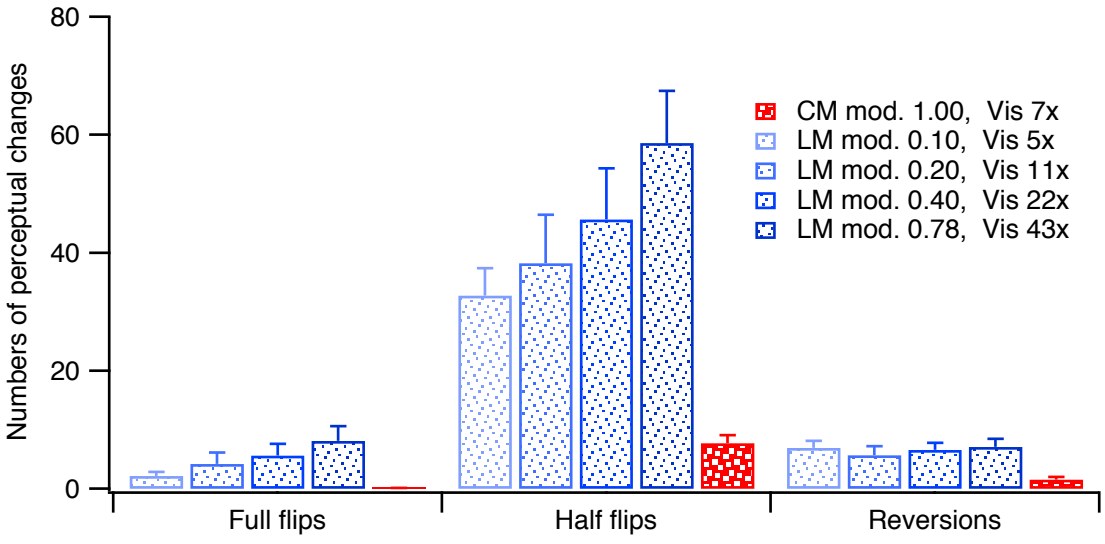

Figure 2.6: Perceptual changes subdivided into full flips, half flips, and reversions. The different blue bars containing small dots indicate the LM stimuli with contrast of 0.10, 0.20, 0.40 and 0.78. The red bars containing big dots represent CM stimulus result from the first experiment. Visibilities for the different stimuli are depicted in the legend. Vertical bars represent +1 standard error.

Figure 2.7 shows that the mean exclusivity duration (representing exclusive percepts) of LM stimuli with a modulation of 0.1 (3.13 s ± 0.76) is significantly longer than that of similarly visible CM stimuli (1.14 s ± 0.60) [$F(1, 4)= 9.88$, $p < 0.05$]. Mean mixed duration for CM stimuli (24.27 s ± 5.85) is significantly greater than for comparable LM stimuli (3.03 s ± 0.38) [$F(1, 4)=13.13$, $p < 0.05$]. Increasing the visibility of LM stimuli reduced the mean exclusivity duration slightly but not significantly [$F(1.60, 6.41)= 4.13$, $p > 0.05$] and did not affect the mean mixed duration [$F(1.03, 4.10)= 0.58$, $p > 0.05$]. As can be seen in Figure 2.7, the variance for the longest duration (CM mixed) is greater than for the other conditions and percepts. In order to homogenise the variance, data were transformed by taking a square root. Statistical analyses of the transformed data revealed the same significance of results as reported above for the original data.

The differences in the relative amounts of exclusively visible percepts for CM compared to LM stimuli are also depicted in Figure 2.8, which shows example rivalry sequences. The higher occurrence of perceptual changes for LM compared to CM stimuli, and longer mixed phases for CM than LM stimuli, can be observed.

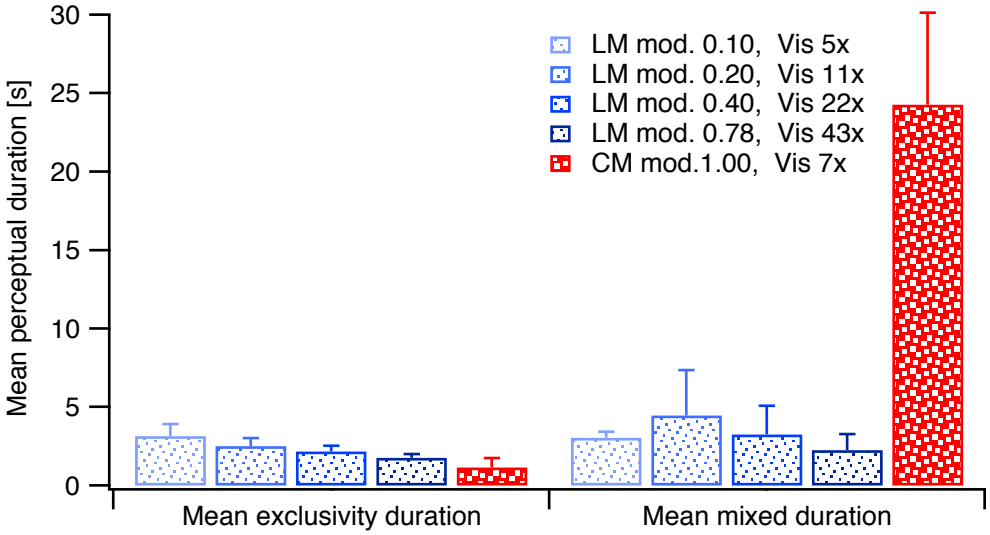

Figure 2.7: Mean durations for LM and CM stimuli. The different blue bars with small dots indicate the LM stimuli with contrast of 0.10, 0.20, 0.40 and 0.78. The red bars with big dots represent CM stimulus result from the first experiment. Visibilities for the different stimuli are depicted in the legend. Vertical bars represent +1 standard error.

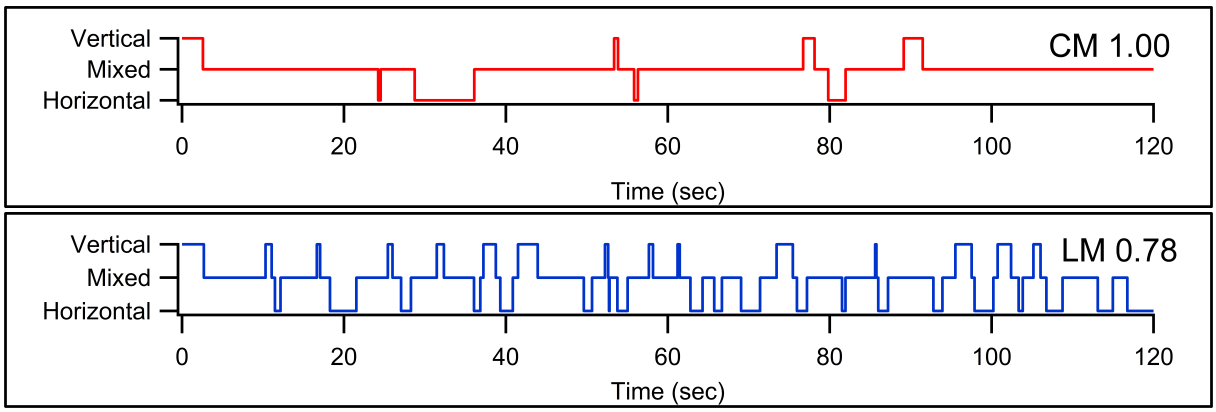

Figure 2.8: Examples of rivalry sequences for single trials of CM stimuli (at a modulation of 1.0) (red) and LM stimuli (at the highest modulation of 0.78) (blue), both at a size of 2 deg and a spatial frequency of 2 c/deg. Exclusive horizontal and vertical percept as well as mixed percept responses are plotted over time.

2.6 Control experiment: monocular grid versus binocular rivalry

The results of the current experimental chapter show low perceptual change rates, very little exclusive visibility and long mixed periods for CM stimuli. With such results, one could ask, whether binocular rivalry actually occurs for CM stimuli or whether the brief periods of exclusivity are the result of other factors such as attention shifts, eye movements and blinks, criterion shifts, local adaptation, and contrast adaptation. These other effects would also influence the perception of a grid presented monocularly. I therefore carried out a subsequent experiment to compare the perception of orthogonally presented gratings separately to the two eyes (binocular rivalry condition described in the main experiments) to the perception of these two orthogonal gratings presented to one eye to form a grid.

2.6.1 Methods

Five new participants were recruited for the experiment; all were unaware of the purpose of the study. The inclusion criteria for the participants as well as the instructions for the task were the same as in the previous experiments. One session included CM and LM binocular rivalry trials, as well as CM and LM monocular grid trials, presented in random order. Eight trials, each lasting at least 120 s, were carried out per condition.

Binocular rivalry stimuli: The sizes for all stimuli were 2 deg with a spatial frequency of 2 c/deg. The contrast for LM stimuli was 0.10 and the modulation depth for CM stimuli 1.00, which represent similar visibility. All other conditions were the same as in the other experiments.

Monocular grid stimuli: The vertical and horizontal gratings were added to produce a grid, and presented to one eye, whilst the carrier noise (with an amplitude of 0.20) was presented to the other eye. Since the horizontal and vertical gratings needed to be (physically) added to create the grid, the modulation depth of each individual grating was half of the one used for the dichoptic presentation, at 0.50 for the CM grating and 0.05 for the LM grating. This ensured that the modulation of the grid at the intersections was the same as the modulation used for each component grating contributing to the dichoptic combination. Based on my previously obtained (unpublished) data, if I had also used the lower modulation for the dichoptic CM gratings, the result would still hold. In this control experiment LM stimuli were presented at a visibility comparable to those of CM stimuli. For each stimulus type, the grid was presented 4 times to the right eye and 4 times to the left eye, in random order.

Analysis: Exclusive visibility was calculated for each participant for 120 s in percent and then averaged across individuals.

2.6.2 Results

The results are shown in Figure 2.9. The CM binocular rivalry condition produced significantly more exclusive percepts, at 13.4 ± 0.5%, than the CM grid condition, at 2.7 ± 1.1 % [$F(1, 4) = 112.07$, $p < 0.001$]. The difference between LM binocular rivalry condition (39.8 ± 8 %) and LM grid condition (5.4 ± 0.9 %) was also significant [$F(1, 4) = 16.45$, $p < 0.05$]. Exclusive visibility reported during the presentation of the LM grid was not significantly different from that for the CM grids [$F(1, 4) = 3.52$, $p > 0.05$].

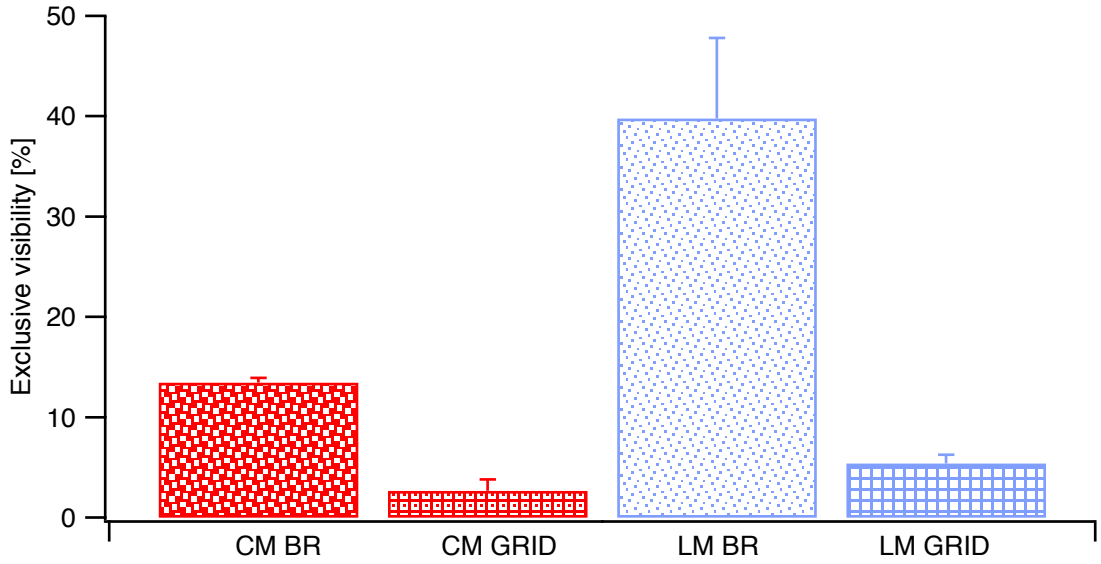

Figure 2.9: Exclusive visibility results in percent for CM (red bar with big dots) and LM (blue bar with small dots) binocular rivalry (BR) and monocular grid conditions (GRID) for CM (red grid pattern with dots) and LM (blue grid pattern) stimuli. Vertical bars represent + 1 standard error.

2.7 Discussion

The experiments reveal that binocular rivalry alternation for CM gratings is very infrequent compared with that for L and LM gratings (Figure 2.3). Exclusive visibility occurs very rarely for CM stimuli and generates significantly longer mixed periods, 15-24 seconds or more, compared to L and LM stimuli (Figure 2.2 and Figure 2.7).

2.7.1 Effect of stimulus size on the characteristics of binocular rivalry

The mild decrease found in exclusive visibility with increasing size for L stimuli revealed in Figure 2.2A has been previously demonstrated (Breese, 1909; Blake et al., 1992; O'Shea et al., 1997). The same pattern was found for LM noise stimuli, which contained added dynamic binary noise, and CM noise stimuli. The reduction in exclusive visibility with an increase of size can be explained by the accompanying reduction of mean exclusivity duration previously demonstrated for L stimuli (Breese, 1909), and an increase in mean mixed duration for all types of stimuli (Figure 2.2C). This is the first study to show that the same relationship holds for CM stimuli. Although strong evidence exists to support separate processing mechanisms

for LM and CM stimuli (e.g. Schofield and Georgeson, 1999; Calvert et al., 2005; Chima et al., 2015), the results described above show that similarities between the two can be observed.

In this study, a full flip represents a change from one exclusive percept to another without a mixed state in-between. The demonstrated decrease of full flips with increasing size for L stimuli (Figure 2.3) is in line with previous experimental results (O'Shea et al., 1997). The same result is shown for LM stimuli in the current experiments. CM stimuli rarely provoked a full flip.

2.7.2 Effect of visibility levels on binocular rivalry

The differences in perceptual changes for L and LM compared to CM stimuli could have resulted from their very different contrasts and thus the visibilities. According to Levelt's fourth law, reducing the contrast of both rival stimuli, reduces the expected rate of perceptual alternation (Levelt, 1965), however this effect may reverse when both stimuli are at the same near-threshold level (Brascamp et al., 2015). Hence, I investigated whether the differences were due to a simple difference in visibility between LM and CM stimuli or due to a higher, more binocular processing mechanism for CM, compared to LM stimuli.

The increase in contrast for LM stimuli leads to an increase in the number of full flips (in agreement with Levelt's modified fourth law (Levelt, 1965; Brascamp et al., 2015)), and half flips (Figure 2.6), and thus to a decrease of the mean exclusivity duration (Figure 2.7). Exclusive percepts for all LM stimuli tend to increase in proportion, over the first 6 s and then stabilise (Figure 2.5). The visual system is accustomed to combining monocular information to a binocular percept. Under binocular rivalry conditions however, neurones are unable to combine different monocular inputs. Instead, the binocular neurones may feedback to the monocular neuronal columns and gradually activate mutual inhibition. Said and Heeger (2013) suggested that this feedback could involve opponency neurones, which receive excitatory input from one eye and inhibitory input from the other eye for each orientation and compute differences between the signals from the two eyes. According to the idea of mutual inhibition as an underlying mediating force of perceptual alternations during binocular rivalry (e.g. Seely and Chow, 2011) and the possible role of opponency neurones (Said and Heeger, 2013), I speculate that 6 s are necessary to gain sufficient neuronal excitation and inhibition in columns of monocular neurones to reach exclusive visibility (or absolute suppression). CM

stimuli do not demonstrate a significant change of perception over time and are mainly perceived as a mixed percept. At a similar visibility (LM at ~5 x detection threshold and CM at ~ 7 x detection threshold) LM stimuli trigger significantly more perceptual changes than CM stimuli.

2.7.3 Why is second-order rivalry different from first-order rivalry?

The most striking finding of the present experimental chapter is the much lower rate of all types of perceptual change as well as the higher proportion of mixed percepts for CM compared to LM stimuli, at a similar visibility (Figures 2.4 and 2.6). Differences in the relative proportion of exclusive visibility between similarly visible LM and CM stimuli result from longer mean mixed durations for CM stimuli (Figure 2.8).

Psychophysical estimates of spatial summation areas are larger, and visual acuity is worse, for CM than for LM stimuli suggesting underlying CM processing mechanisms are larger (Sukumar and Waugh, 2007, Hairol et al., 2013). A stimulus presented to the 'CM system', would seem relatively smaller than the same size stimulus presented to the 'LM system'. Blake et al. (1992) showed that exclusive visibility increases as stimulus size decreases. On this basis more exclusivity should be reported for CM, than for LM stimuli, the opposite of the findings of this chapter. Therefore, the difference in the results for CM and LM stimuli cannot be explained by the two systems operating at different spatial scales.

It has been suggested that binocular rivalry of luminance-defined stimuli might be a result of mutual inhibition of orientation specific monocular neurones (e.g. Blake, 1989; Seely and Chow, 2011; Scocchia et al., 2014). The processing of second-order information may require an additional stage to the processing of first-order stimuli. This has been reflected in the 'filter-rectify-filter' model proposed for the processing of second-order information (e.g. Schofield and Georgeson, 1999; Baker and Mareschal, 2001). Results of single cell (Li et al., 2014), neuroimaging (Larsson et al., 2006, Kim, Kim, Chung, and Wilson, 2007), electrophysiological (Calvert et al., 2005) and psychophysical (e.g. Wong et al., 2001; Sukumar and Waugh, 2007) studies have suggested that the site for this processing of second-order information is beyond V1 and that the neurones involved are binocular (e.g. Wong et al., 2001; Tanaka and Ohzawa, 2006; Hairol and Waugh, 2010). Of particular significance to the current study, is an abstract of a neuro-imaging study by Kim et al. (2007) where the

authors used uncorrelated CM dynamic random-dot fields to generate binocular rivalry. Kim and collaborators suggested that area V2 is specialized in processing second-order stimuli after the researchers found fluctuations in the metabolic activity in V2 but not in V1 during perceptual alternations in binocular rivalry.

One could speculate that the low perceptual change rates and exclusive visibility for CM stimuli are due to the involvement of binocular neurones, in an area beyond V1, that are not orientationally selective and therefore promote mixed perception of orthogonal gratings. However, results of two single-cell studies in macaques' area V1 and V2 showed that these neurones display orientation tuning to CM stimuli (Li et al., 2014; An et al., 2014). Therefore, different neurones process information from the horizontal and the vertical CM grating, but the results of this experimental chapter indicate that they do not engage in binocular rivalry in the same fashion as neurones that initially process LM information.

In fact, the results of the 'binocular rivalry' experiments could mean that orthogonal CM gratings do not rival at all, and any exclusivity reported is the effect of other factors such as eye movements or blinks, attention shifts or adaptation, that have disrupted the perception of the grid formed by the two gratings. However, the results of the 'monocular control' experiment in this chapter (Figure 2.9) show that exclusivity measured during dichoptic presentations is higher than that measured when both gratings are presented to one eye to form a grid. Hence, when orthogonal CM gratings are presented dichoptically to the two eyes, the observed binocular rivalry is very likely to be a result of competition of cortical units. The competition occurs infrequently, which implies that the neurones involved promote combination rather than competition between each other. This is plausible if the neurones that process CM stimuli are binocular.

As previously proposed for luminance stimuli (Lehky, 1995; Brascamp et al., 2006), CM stimuli may sometimes generate exclusivity during binocular rivalry as a result of intrinsic noise. Noise in this context refers to the stochastic variation of system components in the cortex such as vesicular (local neurotransmitter) release variations, spiking variations, and fluctuations in global neurotransmitter level (Moreno-Bote, Rinzel and Rubin, 2007). After the first-order noise is filtered (Schofield and Georgeson, 1999), the second-order grating component needs an additional processing stage, which could also be disrupted because of intrinsic noise (Lehky, 1995; Brascamp et al., 2006) and therefore trigger perceptual

alternation. Visual attention (Lack, 1974; Scocchia, Valsecchi, and Triesch, 2014), and eye movements (van Dam and van Ee, 2006a; b) may also play a crucial role in driving perceptual change during binocular rivalry.

The result of low perceptual change rates for CM stimuli is akin to the results obtained for monocular rivalry (e.g. Breese, 1899; Andrews and Purves, 1997; O' Shea, Parker, La, and Alais, 2009). In the case of monocular rivalry, a stimulus composed of competing elements e.g. orthogonally oriented red and green gratings, will trigger perceptual change when it is viewed monocularly or binocularly. O'Shea et al. (2009) suggested that monocular rivalry is a form of perceptual ambiguity that is mediated by a high-level mechanism (O' Shea et al., 2009). Low rates of CM half and full flips could point to a similar processing site beyond the level of monocular neurones.

During the experimental design and stimulus calibration process, steps to ensure that the second-order stimuli did not contain luminance artefacts were taken (see Section *2.5.1 Methods*), (see also Scott-Samuel and Georgeson, 1999). However, it is possible that a first-order signal may arise from the visual processing of a second-order stimulus. For example, psychophysical responses show an imbalance for black and white luminance processing within second-order stimuli (Lu and Sperling, 2012). This imbalance may introduce a first-order signal into the visual processing of a second-order stimulus. In fact, the low levels of exclusive visibility and flip rate reported for CM stimuli might be expected for low visibility LM stimuli. Therefore, I presented LM stimuli near to their detection-threshold and even for these LM stimuli, exclusive visibility was much higher than for CM stimuli (Figure 2.4).

The results imply that CM stimuli do engage in binocular rivalry but with different characteristics to those found for LM stimuli. The results would agree with suggestions made in previous studies that initial stages for processing of CM stimuli involve a more binocular neuronal population than those engaged in the initial processing of LM stimuli (e.g. Wong et al., 2001; Wong et al., 2005; Hairol and Waugh, 2010; Chima, Formankiewicz and Waugh, 2015).

2.7.4 Role of binary noise in CM stimuli

The current study of this chapter uses correlated binary luminance noise for stimuli presented to both eyes, i.e. noise checks correspond in space, time and luminance in right and left eyes. Studies that investigated the role of noise in the binocular combination of second-order stimuli have reported no significant differences in results obtained with correlated, uncorrelated or anti-correlated noise. Wilcox and Hess (1996) reported no significant differences between stereo-acuity results for uncorrelated and correlated one dimensional noise. Binocular summation of contrast detection thresholds for LM and CM sinusoidal gratings using correlated, uncorrelated and anti-correlated noise produced the same results (Georgeson and Schofield, 2011). Zhou and collaborators measured the perceived phase of binocularly combined LM and CM gratings with correlated, uncorrelated, and anti-correlated noise (Zhou et al., 2014). Again, no significant differences were found between those noise conditions. However, binocular rivalry occurs because the two monocular images differ (e.g. in their orientation). It is possible to increase the difference between the two monocular gratings that were used in the current study of this chapter by removing the binocular correspondence of the noise checks, i.e. by un- or anti-correlating the noise. Orthogonal gratings that contain uncorrelated and, in particular, anti-correlated noise would provide higher potential for binocular rivalry than when the noise is correlated. The difference in luminance between left and right stimulus would provide an additional difference in the first-order input. Kim and collaborators reported in an abstract, that binocular rivalry for CM stimuli can be successfully generated using uncorrelated noise (Kim, Buckthought and Wilson, 2006). It remains unclear, however, whether this alternation was due to the first-order input of the uncorrelated noise, the second-order component, or perhaps both.

2.8 Conclusion

Binocular rivalry can be triggered by both LM and CM grating stimuli using correlated binary noise. The study of this second chapter demonstrated that orthogonal CM gratings presented dichoptically tend to combine with each other for much longer periods than do L and LM stimuli. The results provide further evidence for a different processing mechanism for CM stimuli that tends to encourage binocular combination rather than rivalry.

Chapter 3 - The contribution of piecemeal and superimposed states to perception during binocular rivalry using luminance-modulated and contrast-modulated stimuli under anti-, un-, and correlated noise conditions

A part of this chapter has been published as:

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[http://ecvp.org/2015/AbstractBooklet.pdf]

3.1 Introduction

Binocular rivalry refers to visual competition that arises when different images are presented separately to each eye (e.g. Wheatstone, 1838; von Helmholtz, 1867; Levelt, 1965; Brascamp, Klink, and Levelt, 2015). Visual stimuli such as gratings presented at orthogonal orientations, e.g. a horizontal grating to the left eye and a vertical grating to the right eye, generate perceptual alternations from one exclusively visible grating to the other. However, mixed states of both gratings in one percept can occur in the form of piecemeal rivalry in zones, so that a percept contains portions of each grating (e.g. Blake, O'Shea, and Mueller, 1992), or near contrast detection threshold, orthogonally orientated grating stimuli can overlap, a percept referred to as a 'dichoptic plaid' (Liu, Tyler, and Schor, 1992) or 'superimposition' (e.g. Brascamp, van Ee, Noest, Jacobs, and van den Berg, 2006). If rivalling stimuli with very different spatial frequencies (Yang, Rose, and Blake, 1992) are dichoptically presented, they can begin to superimpose and appear in different depth planes. When the orientational differences between dichoptically presented stimuli are about 10 deg to 22 deg, a mixed percept may be arise that is experienced as "...inclined in depth" (Schor, 1977, page 587).

Piecemeal percepts are suggested to represent rivalry within small spatial zones throughout the visual field. They occur for larger stimuli, but have been described for stimulus sizes as small as 10 arcmin (Blake et al., 1992). Blake and collaborators (1992) designed a model in which rivalry develops via independent, adjacent, non-overlapping interacting retinal areas. Spatial concatenations of multiple zones in different exclusivity states were thought to result in piecemeal percepts during binocular rivalry.

During superimposition both rivalry stimuli are perceived as completely overlapped. It occurs mainly when visibility is close to detection threshold (Liu et al., 1992; Brascamp et al., 2006). Liu et al. (1992) suggested that non-oriented receptive fields might provide an underlying neuronal substrate for superimposition. However, Brascamp and collaborators (2006) showed that superimposition increases gradually as contrasts of rival stimuli are reduced. A separate mechanism for superimposed percepts would be expected to involve an abrupt transition from piecemeal perception to superimposition. Instead, these researchers suggest that binocular rivalry develops gradually from exclusivity, through piecemeal perception, to superimposition. Both groups have suggested that superimposition is an indicator for binocular involvement, or fusion.

Results of neuro-imaging studies have shown no significant metabolic activity in V1 during mixed phases of binocular rivalry for two orthogonally oriented gratings (Polonsky, Blake, Braun, and Heeger, 2000); or for face and grating rivalry stimuli (Lumer, Friston, and Rees, 1998). On the other hand, extrastriate areas in parietal and frontal cortex are metabolically active during piecemeal states of binocular rivalry (Lumer, Friston, and Rees, 1998; Knapen et al., 2011). Visually evoked potentials, measured during binocular rivalry, show highest amplitudes during mixed perception, shortly before perception changed to exclusive visibility (Katyal et al., 2016). The authors suggested that contributions from binocular neurones caused this additional amplitude component at the mixed stage.

Whether an exclusive or a mixed percept occurs during binocular rivalry can depend on low-level stimulus characteristics (i.e. those initially processed in early stages of the visual cortex) such as size (e.g. Breese, 1899; Blake et al., 1992; O'Shea, Sims, and Govan, 1997), contrast (e.g. Levelt, 1965; Bossink, Stalmeier, and De Weert, 1993; Brascamp, Klink, and Levelt, 2015), orientation (e.g. Wade, 1974; Schor, 1977) and spatial frequency (e.g. Kitterle and Thomas, 1980; O'Shea, Sims, and Govan, 1997). The level of stimulus complexity also influences the course of binocular rivalry alternation (e.g. Nguyen, Freeman, and Alais, 2003; Alais and Melcher, 2007). Gratings or circles are considered to have low complexity, whereas houses or faces are thought to be complex stimuli in this context, as they require more cognitive or semantic computation (Lumer et al., 1998, but also Blake and Logothetis, 2002).

All of the studies described above used luminance-based or coloured gratings or objects (so-called first-order spatial stimuli), which are differentiated from their backgrounds by a change of mean luminance or colour. CM noise stimuli (i.e. a type of second-order stimulus) can be perceived even though they do not show any variations of mean luminance across a stimulus but variations in contrast (e.g. Chubb and Sperling, 1988; Zhou and Baker, 1993; Mareschal and Baker, 1999; Schofield and Georgeson, 1999; Landy and Graham, 2004). Results from a number of psychophysical studies (e.g. Schofield and Georgeson, 1999; Hairol and Waugh, 2010; Chima, Formankiewicz, and Waugh, 2015), an electrophysiological study (Calvert et al., 2005), a neuro-imaging study (Larsson, Landy and Heeger, 2006), and neurophysiological studies in cats (Tanaka and Ohzawa, 2006; Mareschal and Baker, 1998) and macaques (An et al., 2014; Li et al., 2014) suggested that additional computation is necessary (compared to first-order stimuli) in order for second-order stimuli to be perceived (e.g. Baker, 1999; Schofield and Georgeson, 1999; Landy and Graham, 2004).

In a previous experiment (see *Chapter 2*), I investigated binocular rivalry characteristics for orthogonally orientated gratings created using sinusoidal modulations of luminance, luminance noise and contrast. I demonstrated that even under comparable visibilities, a higher proportion of mixed perception was evident for rivalling CM than LM stimuli. I suggested that the higher proportion of mixed percepts for CM stimuli might reflect the involvement of more binocular areas of processing for CM, than LM stimuli. However, as noted above, 'mixed' percepts likely consist of both piecemeal and superimposition.

The first aim of the study presented in this chapter is to disentangle specific characteristics of piecemeal and superimposed perceptual states during binocular rivalry, for LM and CM stimuli. If CM stimuli are first processed by units also involved in binocular fusion as suggested by e.g. Wong et al., (2001) and Hairol and Waugh, (2010), I hypothesise that greater proportions of superimposition within the 'mixed' percept should occur and last longer for CM, than for LM stimuli. In a previous experiment, I used interocularly correlated binary noise (see Section *2.2.2 Stimuli*), i.e. black/white pixel checks corresponded in space and time between the eyes. Monocularly opposite luminance information provided by anti-correlated or uncorrelated noise may lead to stronger binocular rivalry. Hence, my second aim is to investigate the effects that different interocular noise correlations have on binocular rivalry characteristics using LM and CM stimuli.

3.2 Methods

All methods described in the following subsections are modifications of the methods in the second chapter of this thesis (see Section *2.2 Methods*).

3.2.1 Observers

Eight male and seven female participants with an average age of 25.7 ± 5.2 years carried out the experiment. Three were experienced in binocular rivalry experiments.

3.2.2 Stimuli

The stimuli were presented in a circular aperture of 2 deg diameter and contained a 2c/deg sinusoidal grating. The left eye's stimulus contained a horizontal grating, and the right eye's, a vertical grating. LM gratings were created by adding dynamic two-dimensional binary noise with an amplitude of 0.2 to a sine-wave with luminance modulation of 0.1. The same noise amplitude was multiplied by the sine-wave to create the CM gratings with a modulation of 1.00. It is important to consider the visibility of stimuli used to generate binocular rivalry since luminance contrast (and therefore visibility) of first-order stimuli influences the course of rivalry (e.g. Levelt, 1965; Brascamp et al., 2015). In an earlier experiment (see Section *2.5.2 Data analysis*), I measured detection thresholds for CM and LM stimuli of the same size, spatial frequency as used in the experiment of the current chapter. Based on these detection thresholds (averaged across participants and observers), for the modulations used in this experiment, the visibilities for the two types of stimuli are similar, at 7 ± 1 (standard error) times and 5 ± 1 times for CM and LM stimuli, respectively.

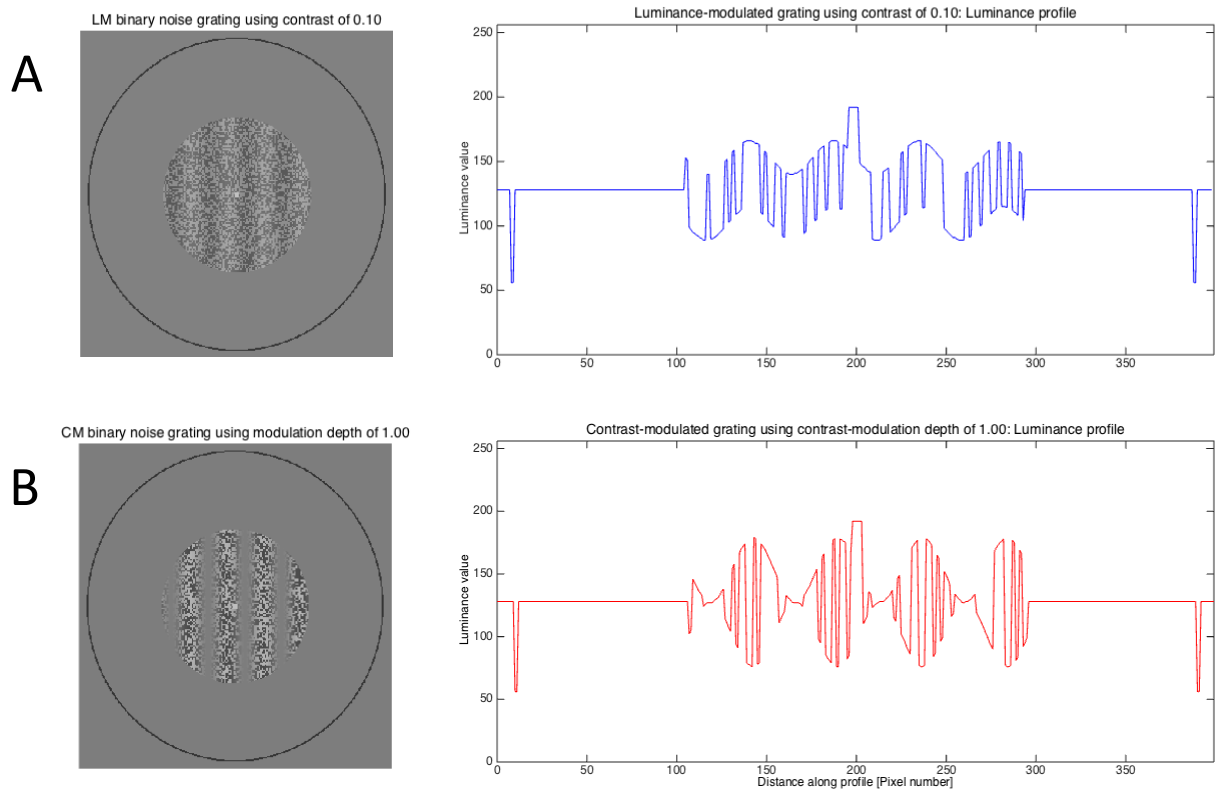

Figure 3.1: Illustration of vertical LM and CM gratings with luminance profiles for a horizontal line of pixels through the centre of the stimulus. A) LM sinusoidal grating with contrast of 0.10 and added two-dimensional binary noise with a contrast of 0.20. B) CM sinusoidal grating with a two-dimensional binary noise carrier, which had its contrast modulated by the grating (modulation 1.00). Both stimuli were surrounded by a fusion lock of a 4 deg diameter and contained a static fixation spot (6x6 pixels) in the centre with a luminance contrast of 0.20.

Stimuli were presented on a grey background with a mean luminance of 48.6 cd/m^2. A surrounding annulus with a diameter of 4 deg and a width of 2.6 arcmin (2 pixels) was used as a fusion lock (Figure 3.1)

Three different noise configurations were used. 'Correlated noise' refers to noise checks that correspond interocularly in space, time and luminance. 'Anti-correlated noise' refers to noise checks that correspond interocularly in space and time, but with opposite luminance values. 'Uncorrelated noise' refers to noise checks that randomly correspond interocularly in space and time; thus, there is a 50 % chance that a particular check in one eye also corresponds in luminance with the same check in the other eye.

3.2.3 Procedure

The task for the participant was to press and hold various button configurations on a response box (Figure 3.2). Participants were instructed to view the fixation spot in the centre of the stimuli and had to press and hold the left button ('A' in Figure 3.2) on a response box when only the horizontal grating (left eye's image) was visible, or the right button when only the vertical grating (right eye's image) was visible ('C' in Figure 3.2). If a percept contained portions of both stimuli, the participant was instructed to press the left and right buttons together ('A' and 'C' in Figure 3.2) for piecemeal perception. When both stimuli completely overlapped, the left, middle and right buttons had to be pressed ('A', 'B' and 'C' in Figure 3.2) to indicate superimposed perception. No button presses or any other button combination indicated invalid responses. Three experimental sessions were carried out, in which different noise configurations were used. Each session included 12 trials for LM and 12 trials for CM stimuli in randomised order. One trial lasted at least 45 s. Instructions and practice trials were given before formal data collection started. Breaks in-between trials were permitted if needed. A complete session lasted between 25 and 45 mins, depending on the breaks for each participant. For each participant, the three sessions were carried out on separate days.

Perceptual change category	**Perceptual changes**
Full flips	H <->V
Half flips	H <->P V <->P H <->S V <->S P <->S
Reversion (total)	H ->P -> H P ->H ->P V ->P ->V P ->V ->P H ->S ->H S ->H ->S V ->S ->V S ->V ->S P ->S ->P S ->P ->S
Within mixed reversion	P ->S ->P S ->P ->S
Gradual flips	H <->P V <->P P <->S
Abrupt flips	Full flips H <->S V <->S

Table 3.1: Perceptual change categories and their respective responses. The perceptual states are indicated as follows: horizontal (H), vertical (V), piecemeal (P) and superimposed (S). The symbol <-> indicates flips between the indicated states whereas the symbol -> is used for all reversion types to indicate a change from one state to another.

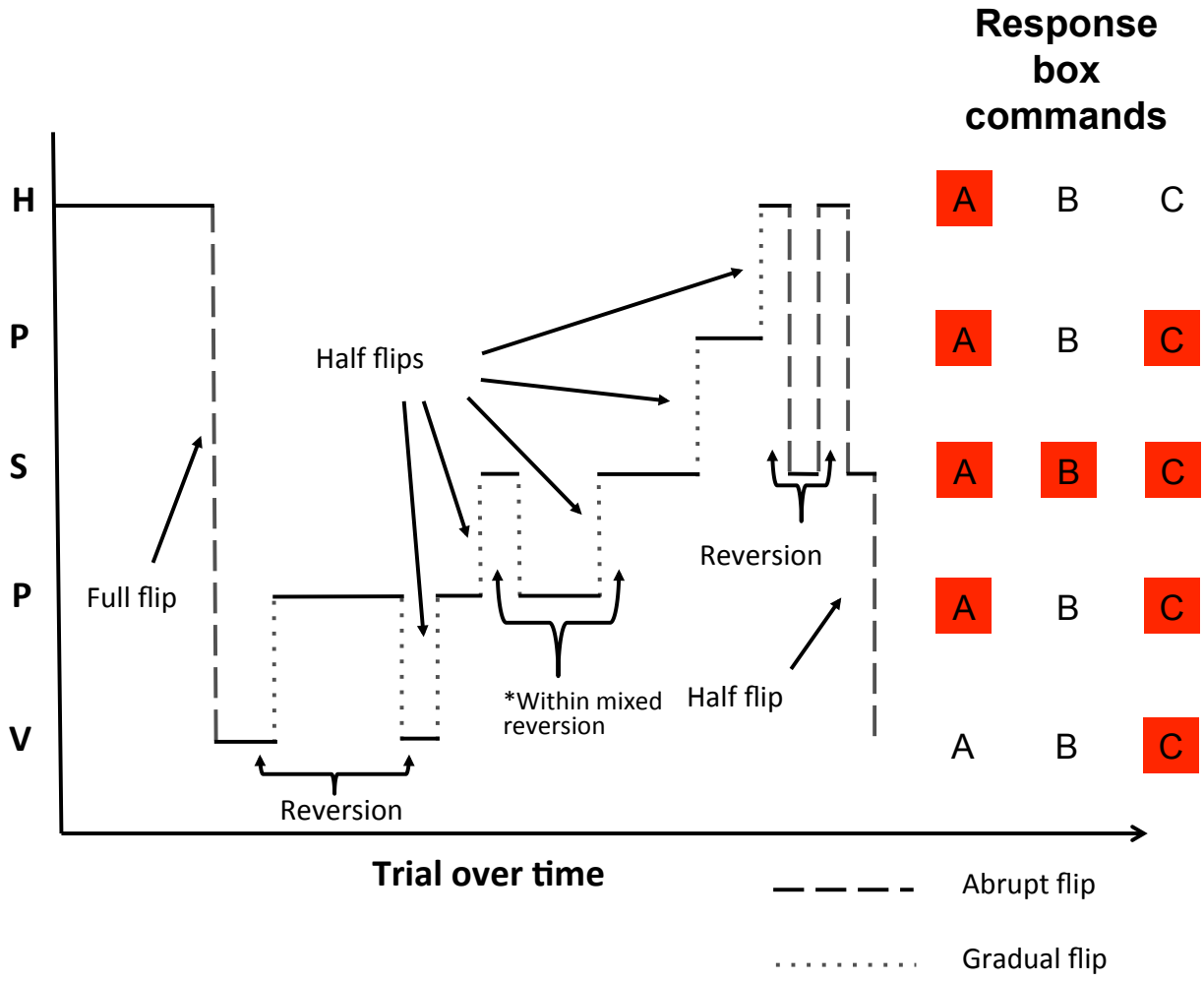

Figure 3.2: Illustration of a binocular rivalry sequence over time and description of the various perceptual change options. The y-axis shows the four response options: exclusive horizontal (H), exclusive vertical (V), piecemeal (P) and superimposed (S). The x-axis represents the trial duration. The letters 'A', 'B' and 'C' marked in red on the right side of the illustration represent the corresponding response box commands. Pressing the button labelled 'A' on the response box signalled that an exclusive horizontal grating was perceived, 'C', that an exclusive vertical grating was perceived. Pressing both 'A' and 'C' referred to piecemeal percepts. Pressing buttons 'A', 'B' and 'C' together indicated that both gratings were perceived completely superimposed. The dashed lines represent abrupt flips and the dotted lines represent gradual flips.

3.2.4 Data analysis

The data were analysed to extract a number of rivalry parameters. Definitions of perceptual change categories are provided in Figure 3.2 and Table 3.1. Perceptual durations of exclusive visibility (sum of responses for the horizontal and the vertical grating), piecemeal and superimposed perception across 45 s and their respective mean durations were calculated. Perceptual state results for 3 s intervals across the trial duration ('3-s-bins') were also calculated to investigate the effects of time on the course of rivalry. The last response of a trial was not included in these calculations, as its duration would have been reduced by the termination of the trial at 45 s. When a percept did not occur during a trial (e.g. a participant never reported an exclusive visible horizontal percept), a duration of 0 s was used in calculating the mean across trials to reflect this.

As I used the same spatial frequency for both gratings and orthogonal grating orientation, I did not expect that participants would perceive a superimposed mixed state with a depth impression (Schor, 1977; Yang, Rose and Blake, 1992). Participants were asked orally whether they experienced that one grating was seen in front of the other during pilot sessions and training trials. No participant reported superimposed percepts with depth impression.

3.2.4.1 Analysis of perceptual phase distributions

The distributions of the various perceptual phase durations were fitted with a gamma distribution using Matlab (Version R2014b). For each condition and each participant, data was first normalised by dividing the phase durations by the relevant mean. These normalised data were then combined across participants. The perceptual phases are presented in the following form using a gamma distribution:

$$f(x|\alpha,\beta) = \frac{1}{\beta^{\alpha}\Gamma(\alpha)}\, x^{\alpha-1}e^{\frac{-x}{\beta}}\,; x > 0, \alpha > 0, \beta \geq 0$$

The gamma function is indicated with $\Gamma(\alpha)$, the 'shape' parameter is α and represents the skewness of the distribution, the 'scale' parameter β scales the distribution along the abscissa and the number of perceptual events x (e.g. Levelt, 1965; Veser, O'Shea, Schröger, Trujillo-Barreto, and Roeber, 2008; O' Shea, Parker, La, and Alais, 2009). The coefficient of determination (R^2) has been used in previous studies (e.g. Logothetis, Leopold, and Sheinberg, 1996; O' Shea et al., 2009; Lunghi and Burr, 2013) as an indicator of how well actual data fit a predicted model; the closer R^2 is to 1, the better fit of the model to the actual data.

3.3 Results

3.3.1 Perceptual states and mean durations

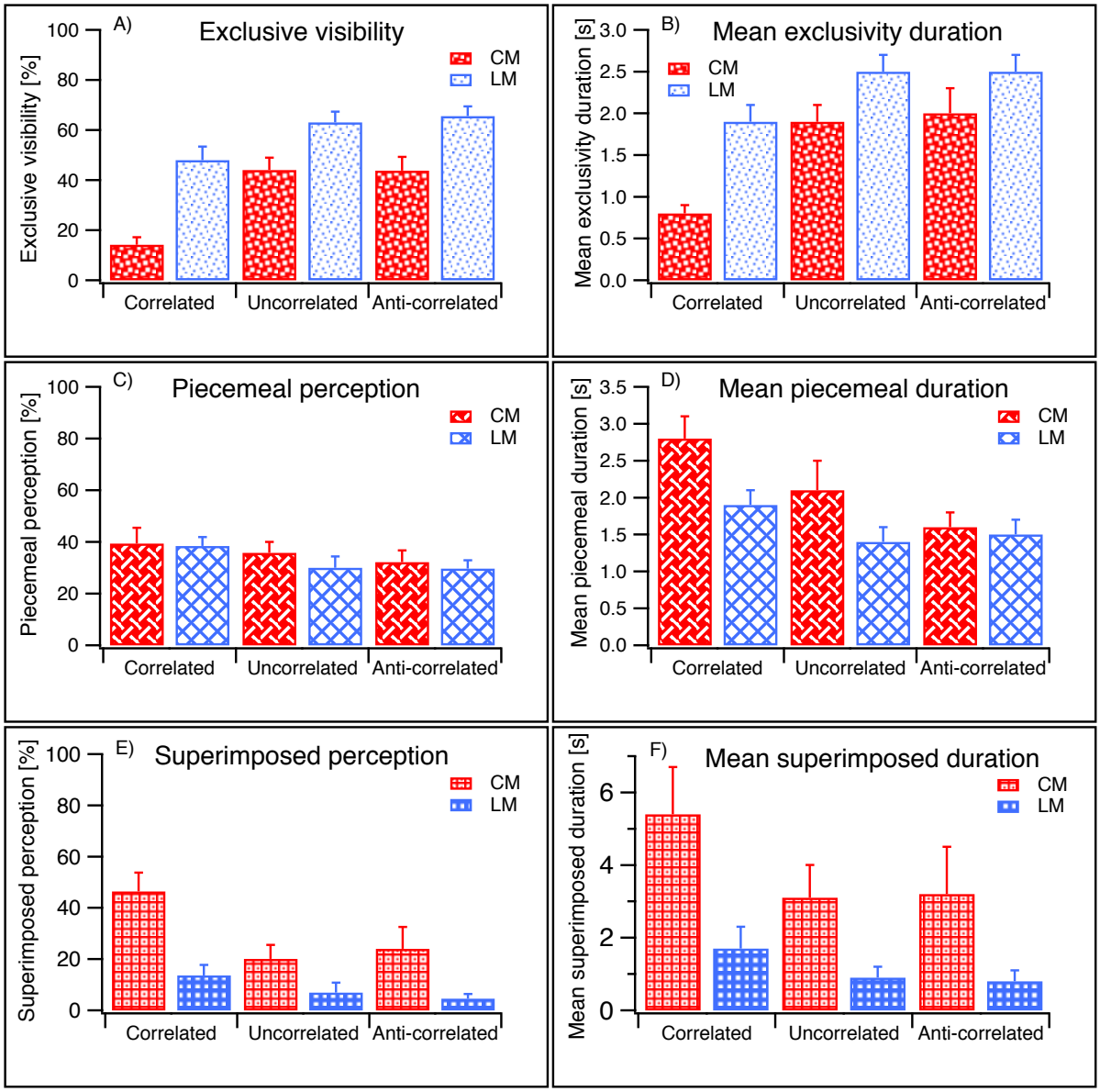

Figure 3.3: Results for the relative proportion of exclusive visibility (A), piecemeal perception (C) and superimposed perception (E) in a trial and their respective mean durations (B), (D) and (F) using interocularly correlated, uncorrelated and anti-correlated noise configurations, averaged across trials and participants. The blue bars with small dots, mosaic-pattern and grid pattern represent percentages and mean durations of exclusive visibility, piecemeal perception and superimposition for LM stimuli, respectively. The red bars with big dots, patchwork pattern and grids with dots indicate percentages and mean durations of exclusive visibility, piecemeal perception and superimposition for CM stimuli, respectively. Error bars indicate + 1 standard error.

The proportions of trial time during which exclusive visibility, piecemeal and superimposed percepts were reported are depicted in Figure 3.3 A, C and E, respectively. As my aim was to investigate the effects of stimulus type and noise configuration on the characteristics of binocular rivalry, I describe and statistically analyse the results for each percept separately.

The proportion of exclusive visibility ranges from 14 ± 3 (standard error) % for CM correlated noise stimuli to 63 ± 4 % and 66 ± 4 % for LM stimuli created using un- and anti-correlated noise, respectively. For both types, but especially for CM stimuli, exclusive visibility is greater for un- and anti-correlated than correlated noise. This differential effect of noise configuration on stimulus type is confirmed by a statistically interaction [$F(1.9, 26.9) = 3.7$, $p < 0.05$]. All LM stimuli generate significantly more exclusive visibility than CM stimuli [planned comparisons, $p < 0.001$]. The differences in exclusive visibility are accompanied by significantly greater proportions of superimposed percepts for CM (from 20 ± 5 % for uncorrelated noise to 46 ± 7 % for correlated noise) than for LM (4 ± 2 % to 14 ± 4 %) stimuli [$F(1,14) = 24.2$, $p < 0.001$]. The proportions of superimposed percepts are also affected by noise correlation [$F(1.7, 24.2) = 7.9$, $p < 0.01$] and are highest with correlated noise. The proportion of piecemeal perception is not significantly different for the two types of stimuli [$F(1, 14) = 0.7$, $p > 0.05$] or three noise configurations [$F(2.0, 27.3) = 1.9$, $p > 0.05$], ranging from 30 ± 4 % to 39 ± 6 %.

Figures 3.3 B, D and F show the mean percept durations. There was a reduction in mean exclusivity duration for both stimulus types as the noise became correlated but again, this effect was greater for CM than LM stimuli [$F(1.9, 26.7) = 3.8$, $p < 0.05$]. The greater proportions of superimposition for CM than LM stimuli are due to the significantly longer mean durations [$F(1, 14) = 15.2$, $p < 0.01$], which averaged across noise are 3.9 ± 1.2 s for CM and 1.2 ± 0.4 s for LM stimuli. CM stimuli also generate longer piecemeal durations compared to LM stimuli [$F(1, 14) = 18.3$, $p < 0.01$]. Duration of superimposed and piecemeal percepts was also affected by noise type [$F(2.0, 27.3) = 3.9$, $p < 0.05$ for superimposed; [$F(1.5, 21.2) = 4.4$, $p < 0.05$ for piecemeal] and was longer with correlated than anti- and uncorrelated noises.

In summary, CM stimuli generate significantly more superimposed percepts than LM stimuli regardless of the noise configuration. Correlated noise engages in shorter moments of

exclusive visibility, but longer phases of superimposed and piecemeal perception for both LM and CM stimuli compared to anti- and uncorrelated noise configurations.

3.3.2 Perceptual changes and reversions

In this section, I compare the effects of stimulus types and noise configuration separately for each of the perceptual changes described in Figure 3.2 and Table 3.1.

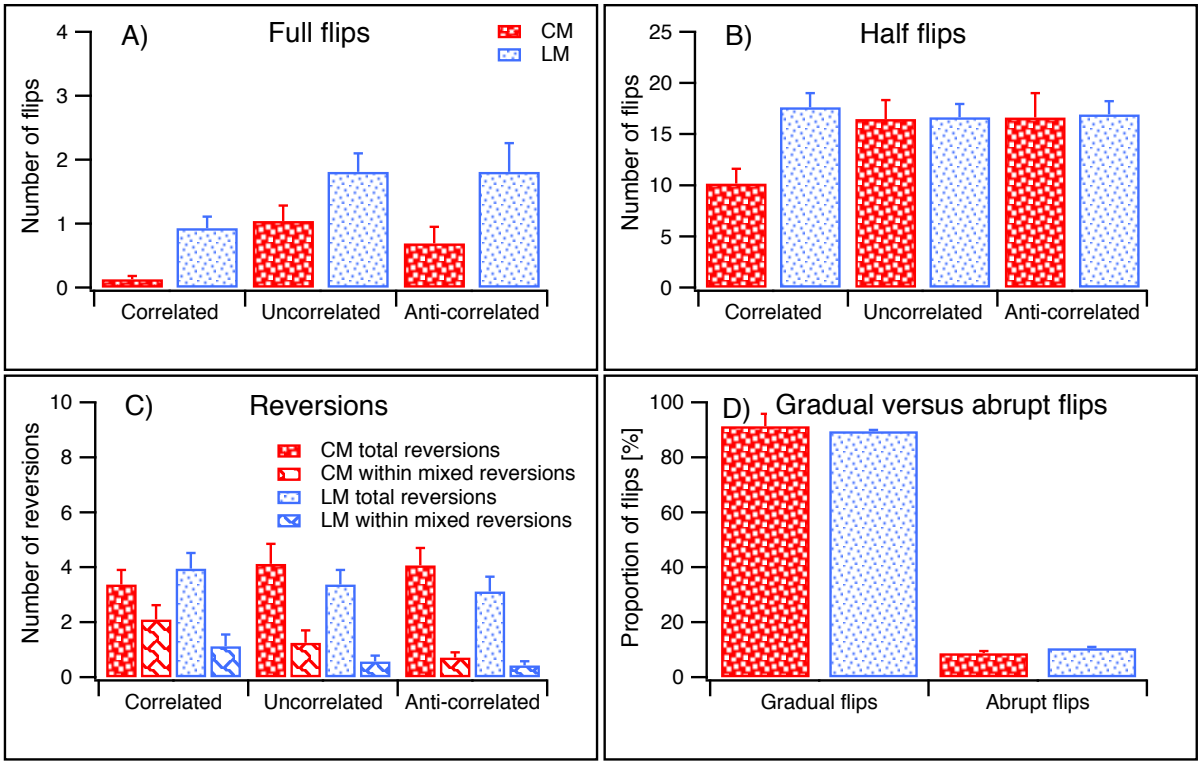

Figure 3.4: Results for number of full flips (A), half flips (B), reversions (C) using interocularly correlated, uncorrelated and anti-correlated noise configurations, averaged across trials and participants. Note the different scale on the y-axes. Gradual versus abrupt flips (D) were averaged across trials and participants, summarised across noise configurations and then divided by the total number (i.e. full flips plus half flips) to get the relative proportions of gradual and abrupt flips. Red bars with big dots represent CM stimuli, blue bars with small dots LM stimuli. The scaled bars in graph C) are within mixed reversions and represent reversions between piecemeal and superimposed percepts, vice versa, for CM and LM stimuli. Error bars indicate + 1 standard error.

Traditionally, binocular rivalry alternation has been described as a change of perception between two exclusive states (e.g. Breese, 1899; Levelt, 1965; O'Shea et al., 1997), which in

the present study are referred to as full flips (Figure 3.4 A). All LM stimuli engage in significantly more full flips than CM stimuli [$F(1, 14) = 12.8$, $p < 0.01$]. An effect of the noise configuration on full flips [$F(2.0, 27.9) = 9.1$, $p < 0.01$] is due to fewer full flips for correlated noise compared to the other two noise configurations. Half flips refer to all changes that are not full flips and occurred more often than full flips. The most striking finding is the lower number of half flips for correlated CM conditions compared to all other stimulus types and noise conditions (Figure 3.4 B). This interaction of stimulus type and noise configuration is statistically significant [$F(1.2, 17.0) = 15.2$, $p < 0.01$] as is the difference between LM and CM stimuli under correlated noise configuration [planned comparison, $p < 0.001$].

During binocular rivalry, perceptual changes from an exclusive percept to a mixed state and back again to the previous exclusive percept are referred to as reversions (e.g. Mueller and Blake, 1989; Brascamp et al., 2006; Robertson, Kravitz, Freyberg, Baron-Cohen, and Baker, 2013). In the paradigm used for the current study, reversions within mixed perceptual states were computed (Figure 3.4 C). In correlated noise conditions, there were slightly more reversions with LM than CM stimuli, whereas the opposite pattern was observed with anti- and uncorrelated noise. This difference in pattern is confirmed by a significant interaction between stimulus type and noise [$F(1.9, 26.1) = 5.9$, $p < 0.01$], but the only statistical significance in the number of reversions for LM and CM stimuli was for the anti-correlated noise configuration [planned comparison, $p < 0.05$]. To the best of my knowledge, the results for reversions within mixed perceptual states (i.e. between piecemeal and superimposed percepts (and vice versa)) have not been presented before. CM stimuli generate more reversions within mixed states than LM stimuli [$F(1, 14) = 8.3$, $p < 0.05$] and correlated noise conditions trigger more of those reversions than anti- and uncorrelated noise configurations [$F(1.8, 24.6) = 5.4$, $p < 0.05$]. I also introduce gradual and abrupt flips as new perceptual change categories (see Scheme in Figure 3.2 and results in Figure 3.4 D). For both stimulus types, the majority of perceptual changes are gradual (90 % for CM and 91 % for LM) rather than abrupt.

3.3.3 Results of perception across time

I analysed the effects of stimulus type and noise configuration on how (and if) the proportion of each percept changes across trial time. Figure 3.5 shows exclusive visibility, piecemeal and superimposed perception analysed across trial time in 3-s intervals for correlated, uncorrelated and anti-correlated noise, for both LM and CM stimuli, averaged across participants. Statistical analyses were performed separately for each percept. Since a trial consists of fifteen '3-s-bins', effects between single intervals might be not revealed with main effect of an ANOVA. Hence, I also performed planned comparisons to analyse differences between single '3-s-bins'.

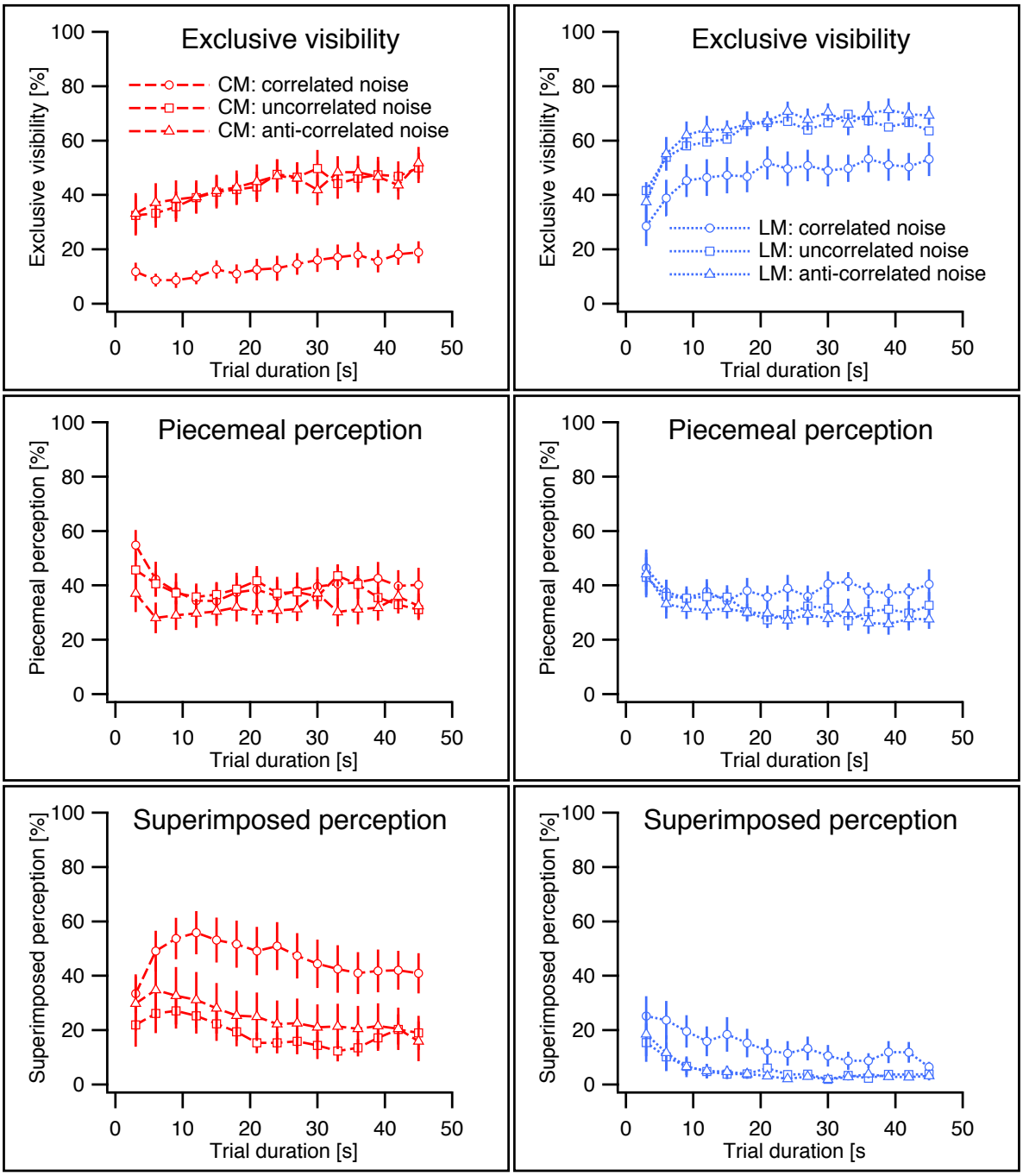

Figure 3.5: Proportion of each perceptual state in 3 s intervals across the 45 s trial for CM (red dashed lines) and LM stimuli (blue dotted lines), and interocularly correlated (circles), uncorrelated (squares) and anti-correlated (triangles) noise configuration. Each data point represents the relative amount of exclusive visibility (top), piecemeal perception (middle) and superimposed perception (bottom) in a 3 s interval, averaged across trials and participants. Error bars indicate ± 1 standard error.

The red and blue functions of Figure 3.5 represent the perceptual states across trial time for CM and LM stimuli, respectively. The proportion of exclusive visibility for CM correlated noise stimuli does not show a definite trend across time whereas it increases gradually for CM un- and anti-correlated noise stimuli. A steep increase is seen over the first few seconds for all LM stimuli. Statistical analysis shows a significant interaction between stimulus type and time [$F(5.4, 75.9)=3.9$, $p < 0.01$], but not between noise configuration and time [$F(7.0, 98.5) = 0.78$, $p > 0.05$]. Planned comparisons confirmed the trends observed in Figure 3.5, i.e. there is a statistically significant [planned comparisons, $p < 0.05$] increase in exclusive visibility from the first to the second, and from the second to the third '3 s bin' for LM but not for CM stimuli.

The proportion of piecemeal perception reduces at the beginning of the trial for all stimuli. Although, overall there is no statistically significant effect of time [$F(1.8, 25.8)=3.0$, $p > 0.05$], on the proportions of piecemeal perception, averaged across participants and noise configurations, the first and second 3 s intervals are significantly different [planned comparisons, $p < 0.05$]. The trend across time for superimposed percepts is different for LM and CM stimuli and this difference is confirmed by a statistically significant interaction between stimulus type and time [$F(3.2, 44.7) = 4.0$, $p < 0.05$]. Over the first 6 s of the trial, averaged across participants and noise configurations, the proportion of perceptual superimposition grows significantly [planned comparison, $p < 0.01$] from 28 ± 8 to 37 ± 8 % for CM stimuli, whereas LM stimuli's perception decreased mildly but not significantly [planned comparison, $p > 0.05$] from 20 ± 8 % to 15 ± 6 %.

3.3.4 Distribution of exclusively visible phases

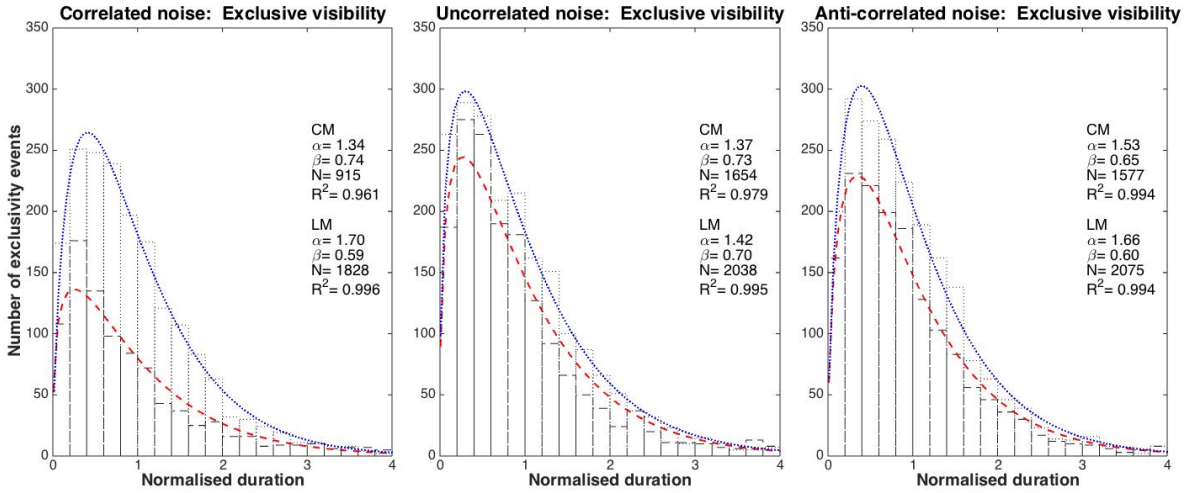

Figure 3.6: LM and CM phase distributions for exclusively visible percepts using interocularly correlated (left), uncorrelated (middle) and anti-correlated (right) noise configurations. The x-axes depict normalised phase durations. The y-axes represent the number of perceptual events. The fitted gamma functions for LM (blue) and CM stimuli (red), parameters of those functions; α - the 'shape' parameter and β - the 'scale' parameter as well as N - the total number of perceptual events are also shown. R^2 is the coefficient of determination.

Figure 3.6 depicts the LM and CM phase duration distribution for exclusive visible percepts using interocularly correlated, uncorrelated and anti-correlated noise. Both CM and LM stimuli phase distributions for exclusive visibility and for all noise configurations show a typical gamma-shape, which has been described as a hallmark of binocular rivalry (Levelt, 1965, 1967; Alais and Blake, 2005). LM stimuli show greater peak values than CM stimuli. Also, interocularly correlated noise CM stimuli generate fewer exclusive events than all other stimulus type/noise configurations, which is another metric that might indicate different processing sites for CM stimuli when first-order input is absent (which means in the context of this experiment no anti-or uncorrelated noises). The coefficient of determination, indicated by R^2 values, is overall closer to 1 for LM compared to CM stimuli.

3.4 Discussion

The experiments have shown that under all noise configurations, but in particular for correlated noise, rivalrous CM stimuli engage in significantly less exclusive visibility and more superimposition than LM stimuli do. The interocular anti- or uncorrelation of noise checks increases the amount of exclusive visibility compared to correlated noise especially for CM, but also for LM stimuli. Piecemeal perception was unaffected by changes of stimulus type and noise configurations (Figure 3.3). The results also demonstrated that the use of LM stimuli triggers significantly more full and half flips than the use of CM stimuli does (Figure 3.4) and that regardless of the stimulus type or interocular noise configuration, more gradual than abrupt flips occur (Figure 3.4). In the following sections I discuss the findings of the current chapter and use them to establish a framework that aims to address the differences between LM and CM binocular rivalry.

3.4.1 Mixed states during LM and CM binocular rivalry

Previously, I reported that CM stimuli created with interocularly correlated noise generate many more mixed percepts (i.e. sum of superimposed and piecemeal percepts) than do LM stimuli (see *Chapter 2*). In the current study, I subdivided mixed states into piecemeal and superimposed perceptual states to investigate these for LM and CM binocular rivalry. It has been suggested that piecemeal perception is rivalry in local zones (Blake et al., 1992) whereas superimposed perception indicates binocular fusion (e.g. Liu et al., 1992; Brascamp et al., 2006).

Several neuro-imaging scholars have investigated the role of mixed, sometimes also referred to as transient, phases during binocular rivalry. It has been shown that mixed perceptual states generate metabolic activity in extrastriate brain regions (Lumer et al., 1998; Polonsky, Blake, Braun, and Heeger, 2000; Knapen et al., 2011), but not in the early visual cortex V1 (Lumer et al., 1998; Polonsky et al., 2000). However, in these studies, the authors did not distinguish between piecemeal rivalry and superimposition. It might be possible that superimposed percepts activate certain areas in the cortex beyond V1, which process binocular summation or fusion information, specifically for the intersectional areas of the superimposed percept, which can appear darker or lighter than the rest of the gratings (Liu et al., 1992).

In the current study, I found significantly greater proportions of superimposed percepts for CM than LM stimuli for all noise configurations, due to longer mean superimposed durations (Figure 3.3 E and F). This result might be expected if superimposed perception has a more binocular processing site compared to piecemeal rivalry (Liu et al., 1992; Brascamp et al., 2006; Klink, Brascamp, Blake, and van Wezel, 2010; Klink, Brascamp, Blake, and Wezel, 2010a, but see also Blake et al., 1992) and if CM stimuli are initially processed in areas of the cortex, which receive greater binocular input than those processing LM stimuli (e.g. Wong, et al., 2001; Sukumar and Waugh, 2007; Hairol and Waugh, 2010) .

Neither noise configuration nor stimulus type showed significant effects on piecemeal perception (Figure 3.3 C). In the task I used, participants had to indicate whether they saw exclusively horizontal or vertical gratings, an absolutely superimposed percept or a piecemeal percept. However, some participants reported that during the indication of 'piecemeal perception', non-overlapping portions of single gratings (piecemeal rivalry) and portions of overlapped gratings (superimposition) were observed (see Appendix *6.2 Current and modified view on perceptual states during binocular rivalry*). Reports suggested that during the 'piecemeal perception' response, CM stimuli were perceived with mainly superimposed percepts whereas LM stimuli were perceived in a mainly piecemeal fashion. These reports would fit in with the main result of more superimposition for CM than LM stimuli. This new perceptual state, which contains portions of piecemeal and superimposition, would also fit into the idea of the gradual evolution of binocular rivalry (Brascamp et al., 2006) as it would be an 'bridge-state' between (pure) piecemeal rivalry and (absolute) superimposition.

3.4.2 The effect of binary two-dimensional noise on the course of binocular rivalry

Interocular noise configurations were varied in the current study. I used 1) correlated noise, i.e. noise checks corresponded in time, space and luminance, 2) anti-correlated noise, i.e. noise checks corresponded in time and space, but the luminance information of noise checks did not correspond and 3) uncorrelated noise, i.e. noise checks corresponded in time and space, but luminance values corresponded (correlated) or did not correspond (anti-correlated) with a chance of 50%.

Studies examining the effects of different interocular noise configurations on the perception of second-order stimuli have been carried out. It has been reported that stereopsis thresholds were not significantly different when one dimensional uncorrelated and correlated noise was used (Wilcox and Hess, 1996). The binocular summation of contrast detection thresholds for LM and CM sinusoidal gratings using correlated, uncorrelated and anti-correlated noise were also not significantly different (Georgeson and Schofield, 2011). Studies concerning the phase of binocularly combined LM and CM stimuli also showed no significant differences in results obtained with correlated, uncorrelated and anti-correlated noise configurations (Zhou, Georgeson, and Hess, 2014; Zhou, Liu, et al., 2014).

The results in Figure 3.3 show that binocular rivalry characteristics of CM stimuli are affected by the nature of interocular noise correlation. When noise is fully correlated, the carrier in one eye contains identical information in time, space and luminance as the other eye. In the context of the CM filter-rectify-filter processing model, the carrier is filtered in the first processing stage and then rectified. In the second stage, the envelope is filtered and either binocularly summed (superimposed perception) or suppressed (piecemeal perception or exclusive visibility). When noise is interocularly anti- or uncorrelated, incompatible luminance information is present at any position for a certain period of time. Hence, the greater proportions of exclusively visible percepts (Figure 3.3 A) and greater amount of full and half flips (Figure 3.4) are likely to be due to competing carrier information, which adds to the conflict of the competing envelopes. This result is interesting since one could ask why then do CM stimuli with identical orientation but with anti-correlated noise not rival (Georgeson and Schofield, 2011). If CM carriers contain rivalling information (interocularly anti- or uncorrelated noise) but the envelopes show identical orientation, then no binocular rivalry but regular binocular combination arises (Georgeson and Schofield, 2011). If the CM carriers are identical (interocularly correlated noise), but the envelopes are orthogonally orientated, then little but significant binocular rivalry occurs (see Section *2.7.3 Why is second-order rivalry different than first-order rivalry?*). In the current chapter, I demonstrate that when both carrier and envelope contain rivalling information, strong perceptual alternation and exclusive visibility for CM stimuli arises. These results suggest that the envelope information plays a key role for triggering perceptual competition for CM stimuli. I suggest that interocular competition between monocular neurones of the first processing stage adds to the competition of the envelopes in the second processing stage, which may feedback to the first processing stage and results in greater perceptual alternation between percepts and more

exclusively visible events for CM stimuli (Figure 3.3 A, Figure 3.4 A and 3.4 B). I proposed previously (see Section *2.7.3 Why is second-order rivalry different than first-order rivalry?*) that orientation-selective neurones are the predominant source of pure CM binocular rivalry since results of single cell studies in macaques demonstrated that cells in V1 and V2 are sensitive to different CM and LM orientations (An et al., 2014; Li et al., 2014). Additionally, I suggest that the increase of perceptual alternations and greater proportions of exclusive visibility, when adding first-order input (via anti-and uncorrelated noise) to a second-order signal, is due to competition of neurones in early visual cortex as results of neuro-imaging studies have demonstrated that exclusive dominance phases during binocular rivalry strongly activate metabolic signals in V1 (Tong and Engel, 2001; Lee and Blake, 2002, but see also Haynes and Rees, 2005) and lateral geniculate nucleus (LGN) (Wunderlich, Schneider and Kastner, 2005; Haynes, Deichmann and Rees, 2005).

3.4.3 Perception of LM and CM stimuli over time

Exclusive percepts for all LM stimuli increase in proportion over the first 6 s and then stabilise (Figure 3.5). For CM stimuli, exclusive visibility changes very little over time when correlated noise is used, but increases over time when anti- or uncorrelated noise is used. This increase may be due to the rivalling first-order input provided by the luminance noise. I have previously speculated that 6 s are necessary to gain sufficient neuronal excitation and inhibition in columns of monocular neurones to reach exclusive visibility (or absolute suppression) for LM stimuli (see Section *2.7.2 Effect of visibility levels on binocular rivalry*). The current results are in line with this suggestion.

The trend of piecemeal perception across time is again similar for LM and CM stimuli, in that there is a mild decrease over the first 6 s of a trial. However, the results for the two types of stimuli are different for superimposed percepts: the proportion of superimposition increases at the beginning of the trial for CM stimuli, but decreases for LM ones. This result emphasises again the possibility of different processing sites of LM and CM stimuli as superimposed percepts are thought to be processed by binocular neurones (Liu et al., 1992; Brascamp et al., 2006), perhaps at the same processing level that has been suggested to be involved in extracting CM envelopes (e.g. Wong et al., 2001; Hairol and Waugh, 2010; Chima et al., 2015).

Klink et al. (Klink, Brascamp, Blake, and van Wezel, 2010a; Klink, Brascamp, Blake, and Wezel, 2010b) showed that piecemeal perception, generated by luminance-modulated, noiseless orthogonal grating and house/face stimuli, tends to be constant over longer periods of time (>800s) whilst superimposed perception increases significantly and suggested that superimposition is a result of weak inhibitory gain. I speculate that 45 s might not be sufficient to stimulate neurones, which are processing binocular input (and are responsible for superimposed percepts), but instead still engage in inhibitory gain.

3.4.4 Distribution of exclusively visible phases

All exclusive visibility phase distributions show the typical gamma shape that has been reported previously for binocular rivalry (e.g. Fox and Herrmann, 1967; Levelt, 1965, 1967; Brascamp et al., 2015) and other ambiguous percepts (e.g. Borsellino, De Marco, Allazetta, Rinesi, and Bartolini, 1972; De Marco, Penengo, and Trabucco, 1977; Kleinschmidt, Buchel, Zeki, and Frackowiak, 1998; Carter and Pettigrew, 2003; Murata, Hamada, Kakita, and Yanagida, 2004; Pastukhov and Braun, 2008; O' Shea et al., 2009) even though other distributions may also represent exclusively visible phase distribution during binocular rivalry (Cogan, 1973; Lehky, 1995; Zhou et al., 2004; Shpiro, Moreno-Bote, Rubin, and Rinzel, 2009). These results throughout different multi-stable perceptual phenomena were thought to be a measure for a common underlying processing mechanism (e.g. Zhou et al., 2004; Murata et al., 2004; O' Shea et al., 2009), however, the potential meaning of gamma-distributed phase durations has also been doubted (Arnold, 2011). The gamma distribution for CM stimuli using correlated noise showed much smaller peak values than all other exclusive visibility gamma phase distributions due to the lowest number of events. These results may support the suggestions of different processing mechanisms for LM and CM stimuli (e.g. Schofield and Georgeson, 1999; Waugh, Lalor, and Hairol, 2009; Chima et al., 2015). I consider pure second-order rivalry to occur only in the correlated noise condition. The coefficient of determination (R^2) has been used in previous studies (e.g. Logothetis, Leopold, and Sheinberg, 1996; O' Shea et al., 2009; Lunghi and Burr, 2013) as an indicator of how well actual data fit a predicted model; the closer the value R^2 is 1, the better the fit. The results show gamma distributions with R^2 values close to 1 for both exclusively visible CM and LM stimuli (Figure 3.6). The poorest fit occurred when CM stimuli were presented under correlated noise conditions, which is likely to be due to the low number of flips (Figure 3.4A).

3.4.5 Why do CM stimuli engage in more superimposition than LM stimuli?

The highlight of the third experimental chapter is that CM stimuli generate significantly more superimposed percepts than do LM stimuli. But how does this result fit into the current view of binocular rivalry dynamics? Double-well or energy landscape illustrations have been used to metaphorically describe the dynamics of perceptual alternations during binocular rivalry (e.g. Brascamp et al., 2006; Kim et al., 2006; Moreno-Bote et al., 2007; Rubén Moreno-Bote, Shpiro, Rinzel, and Rubin, 2010; Pastukhov and Braun, 2011; Seely and Chow, 2011; Kang and Blake, 2011). Well-established models of binocular rivalry describe a mediator-mechanism often called mutual or reciprocal inhibition (e.g. Blake, 1989; Kang and Blake, 2011; Seely and Chow, 2011). The models are based on the assumption that different populations of neurones compete with each other during binocular rivalry. During phases of exclusive visibility, the dominant neural populations are inhibiting neural populations of the other eye's stimulus completely. Following the idea of mutual inhibition, various reasons for perceptual alternation were postulated. One idea is that neural adaptation weakens the dominant stimulus over time and decreases its suppressive impact on the suppressed stimulus until a point of equal system states, which eventually leads to an abrupt change with short transient (mixed perceptual) phases (Lehky, 1988; Mueller, 1990; Kalarickal and Marshall, 2000; Laing and Chow, 2002; Wilson, 2003; Blake, Tadin, Sobel, Raissian, and Chong, 2006; Lankheet, 2006; Seely and Chow, 2011). This is illustrated in Figure 3.7A. The state potential changes as a result of adaptation and the actual system (perceptual) state (red circle), moves between the two exclusive states, represented by the two minima.

Another hypothesis is based on the assumption that random intrinsic noise within the visual system is the driving force for perceptual alternation (e.g. Brascamp et al., 2006; Kim et al., 2006; Rubén Moreno-Bote, Rinzel, and Rubin, 2007; Webber and Bressloff, 2013). The noise model is illustrated in Figure 3.7B, where the potential remains constant, but intrinsic noise of the system triggers the perceptual alternation between the two minima, i.e. the two exclusivity states.

The adaptation model also implies a rapid change between the two exclusive states, but the existence of reversions and mixed periods argues against this idea as previously noted by Brascamp et al. (2006). Hence, Brascamp and collaborators suggested intrinsic noise as a crucial factor for the results of binocular rivalry under low contrast conditions (Figure 3.7C).

The minima tend to be shallow under low contrast and thus generate long mixed durations (as reported by e.g. Liu et al., 1992) when perceptual state (red circle) reaches the transition region. The findings of many more gradual than abrupt flips (Figure 3.4 D) are in line with the idea of intrinsic noise as a predominant cause for perceptual alternation during binocular rivalry. However, both the adaptation and noise models, do not address the fact that reversions occur between piecemeal and superimposed percepts (Figure 3.4C). Therefore, I suggest in Figure 3.7D, a framework that incorporates piecemeal (P) and superimposed perception (S) within the transient region with a third well representing superimposition potential. The minimum of S within the transient region depends on various stimulus characteristics such as the stimulus type reported here (CM or LM), but also on other stimulus characteristics such as size (e.g. Breese, 1899; Blake et al., 1992; O'Shea, Sims, and Govan, 1997), contrast (e.g. Liu et al., 1992; Brascamp et al., 2006; Brascamp et al., 2015), orientation (e.g. Wade, 1974; Schor, 1977), stimulus complexity (e.g. Alais and Melcher, 2007) and spatial frequency (e.g. Livingstone and Hubel, 1987; O'Shea et al., 1997). Earlier in this chapter, I reported that a new perceptual state occurred, which contained portions of superimposed and piecemeal gratings. This bridge-state might be represented right before the potential develops its S minimum. The greater proportions of superimposed percepts under comparable visibility for CM stimuli also suggest noise as the driving force for perceptual alternation, but that the minimum of the S region is much deeper than its LM counterpart (Figure 3.7E).

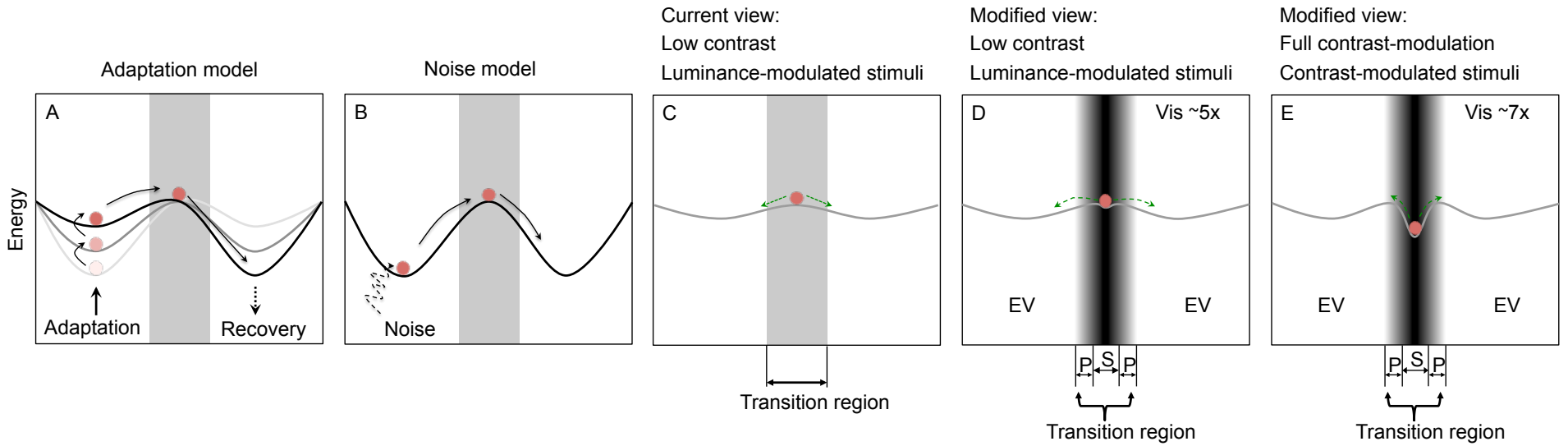

Figure 3.7: Metaphorical demonstration of first-and second-order binocular rivalry dynamics using a double well potential model adapted from Brascamp et al. (2006) and Pastukhov and Braun (2011). The grey zones in the centre of the boxes A-C depict the transient or mixed perceptual region. The black wavy lines in the graphs A and B represent the state potential; the minima of each potential represents exclusive visibility (attractors). The red circle represents the actual system (perceptual) state. A) Adaptation model: The landscape changes over time due to adaptation (thick black line with arrow pointing up) of the current perceptual state and the simultaneous recovery (thick black dashed-line with arrow pointing down) of the suppressed state. B) Noise model: The potential remains constant, however, intrinsic noise of the system (curved-dashed arrow) drives the red circle into the other state potential. C) Current view of binocular rivalry dynamics under low contrast conditions (Brascamp et al., 2006; Pastukhov and Braun, 2011). The deterministic forces, due to intrinsic noise, are weak and the system state may develop in either direction (green dashed arrows). D) The illustration shows the different mixed states in a gradual evolution (represented in the gradual change from white to black) from exclusivity (EV) to piecemeal (P) to superimposition (S), an idea suggested by Brascamp et al. (2006), but not incorporated in to any energy landscape model. The minimum of S depends on various stimuli characteristics e.g. size, contrast, spatial frequency etc. Under the LM stimulus conditions of the current study, mixed perception occurred mainly in a piecemeal fashion, hence S minima level is relatively shallow compared to the CM stimuli condition illustrated in E) Using comparable visibilities between CM and LM stimuli, the minimum of S is deeper for CM than for LM stimuli (approximately 3 times under the current stimulus conditions derived from differences of superimposition for LM and CM stimuli (Figure 3 E)).

3.5 Conclusion

The results of this chapter demonstrate that changes in noise configurations affected binocular rivalry for LM, but in particular CM stimuli. Regardless of noise configuration, CM stimuli generated fewer portions of exclusive percepts and greater portions of superimposed percepts than LM stimuli. Under all noise configurations, CM stimuli alternated less than LM stimuli as they trigger fewer full flips than do LM stimuli. Moreover, CM stimuli perception during binocular rivalry compared to LM stimuli developed differently over time for superimposed perception. The greater proportions of superimposed percepts for CM compared to LM stimuli suggest that the CM envelope component is processed by neurones, which compute initially binocular, rather than monocular information. Orthogonally presented CM envelopes engaged in stronger binocular rivalry alternation if interocular carrier noises were not correlated, which suggests feedback signals between neurones processing envelope information and neurones processing carrier information. I also presented a modified model for binocular rivalry alternation, which takes into account the existence of superimposition and piecemeal perception as well as reversions between these perceptual states.

Chapter 4 - Contrast-modulated stimuli in competition with luminance-modulated stimuli under binocular rivalry conditions

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[http://jov.arvojournals.org/article.aspx?articleid=2551186&resultClick=1]

4.1 Introduction

The normal human visual system combines information received by each eye into a binocular percept as long as the information in the two eyes is similar. However, when the two monocular inputs are very different, interocular competition of perception can occur, known as binocular rivalry (e.g. Wheatstone, 1838; von Helmholtz, 1867; Tong, Meng, and Blake, 2006). Monocular and interocular differences in stimulus properties such as size (Blake et al., 1992; Breese, 1899), colour (e.g. Knapen, Kanai, Brascamp, van Boxtel, and van Ee, 2007), spatial frequency (e.g. O'Shea, Sims, and Govan, 1997), and stimulus complexity (e.g. grating or object stimuli (e.g. Nguyen, Freeman, and Alais, 2003, but see also Kovács, Papathomas, Yang, and Feher, 1996)) affect the characteristics of binocular rivalry. Levelt (1965) proposed four laws concerning the influence of luminance contrast, which he referred to as 'stimulus strength', on the course of binocular rivalry. Stimulus strength refers to the physical stimulus property, which determines the ability of one eye's stimulus to suppress the other.

After the publication of Levelt's thesis, the laws were the subject of many studies (e.g. Fox and Rasche, 1969; Bossink, Stalmeier and De Weert, 1993; Klink, van Ee and van Wezel, 2008), which led to some modifications and specifications of his original laws (see Section *1.2.1 Exclusive visibility, predominance, mean duration and alternation rate*). A recent review (Brascamp et al., 2015) updated Levelt's laws to take into account the current state of knowledge. Levelt's modified four laws are:

"I. Increasing stimulus strength for one eye will increase the perceptual predominance of that eye's stimulus.
II. Increasing the difference in stimulus strength between the two eyes will primarily act to increase the average perceptual dominance duration of the stronger stimulus.
III. Increasing the difference in stimulus strength between the two eyes will reduce the perceptual alternation rate.
IV. Increasing stimulus strength in both eyes while keeping it equal between eyes will generally increase the perceptual alternation rate, but this effect may reverse at near-threshold stimulus strengths." (Brascamp et al., 2015, page 27)

Specifically, the first, second, and third modified laws describe the effects of varying the interocular differences in stimulus strength (e.g. by changing the contrast, blur level or colour

of one stimulus) whereas the fourth modified law describes the impact of binocular stimulus strength variations.

The studies mentioned above used luminance-defined stimuli, which can be distinguished from the background by variations in luminance. Stimuli can also differ from their background by variations of contrast, but not affect mean luminance level. Such stimuli are called contrast-modulated (CM) and several results of psychophysical (e.g. Schofield and Georgeson, 1999; Waugh, Lalor, and Hairol, 2009; Chima, Formankiewicz, and Waugh, 2015), electrophysiological (Calvert et al., 2005), neuro-imaging (Larsson, Landy and Heeger, 2006) and neurophysiological studies in cats (Mareschal and Baker, 1998; Tanaka and Ohzawa, 2006) and macaques (An et al., 2014; Li et al., 2014) have led to the suggestion that additional neuronal computation is necessary to perceive CM compared to luminance-modulated (LM) stimuli. Results of psychophysical investigations have shown evidence for a substantial involvement of binocular neurones during the initial processing of CM stimuli (e.g. Wong et al., 2001; Hairol and Waugh, 2010; Chima et al., 2015; Chima et al., 2016).

I have already shown (in *Chapter 2*) that orthogonally presented CM stimuli also engage in binocular rivalry but when the noise is the same in the two eyes (i.e., correlated), very few moments of exclusive visibility are perceived, compared to binocular rivalry of LM stimuli. Furthermore, CM stimuli generate significantly more superimposed percepts than LM stimuli, implying a substantial involvement of binocular neurones for CM processing (see *Chapter 3*). Interestingly, the amount of superimposition for CM stimuli could be decreased and exclusive visibility increased, accompanied by an increase of the alternation rate, when the interocular correspondence of the noise checks was disrupted. These results imply that binocular rivalry is predominately caused by first-order input (see Section *3.4 Discussion*).

The main aim of the current set of experiments is to test whether LM and CM stimuli rival with each other and if so, to investigate the effects of unilateral and bilateral changes of stimulus strength in respect to Levelt's modified laws. I address this aim in the first experiment by presenting a CM grating to one eye and an orthogonally orientated LM grating to the other, and varying the contrast of LM stimuli across trials. The visibility level was determined by an approximation of multiples over detection threshold as a measure of stimulus strength (for more details see Section *2.5 Control experiment: effect of visibility levels*). If CM and LM stimuli involve different processing sites, then Levelt's laws,

demonstrated for a wide range of noiseless LM stimulus conditions (see review Brascamp, Klink and Levelt, 2015), may not hold. In the second experiment, I wanted to address the question of whether variations of stimuli strengths for competing orthogonal CM stimuli also follow Levelt's laws.

The insights gained by investigating binocular rivalry characteristics when LM and CM stimuli compete with each other will contribute to the ongoing debate of whether binocular rivalry arises early, later or perhaps in multiple visual areas of the brain (e.g. von Helmholtz, 1867; Blake, 1989; Logothetis, 1998a; Frank Tong et al., 2006).

4.2 Methods

All methods described in the following subsections are modifications of the methods in the second chapter of this thesis (see Section *2.2 Methods*). Specific modifications are detailed below.

4.2.1 Observers

Five male and five female adults with an average age of 22.9 ± 4.3 years participated in the experiment.

4.2.2 Stimuli

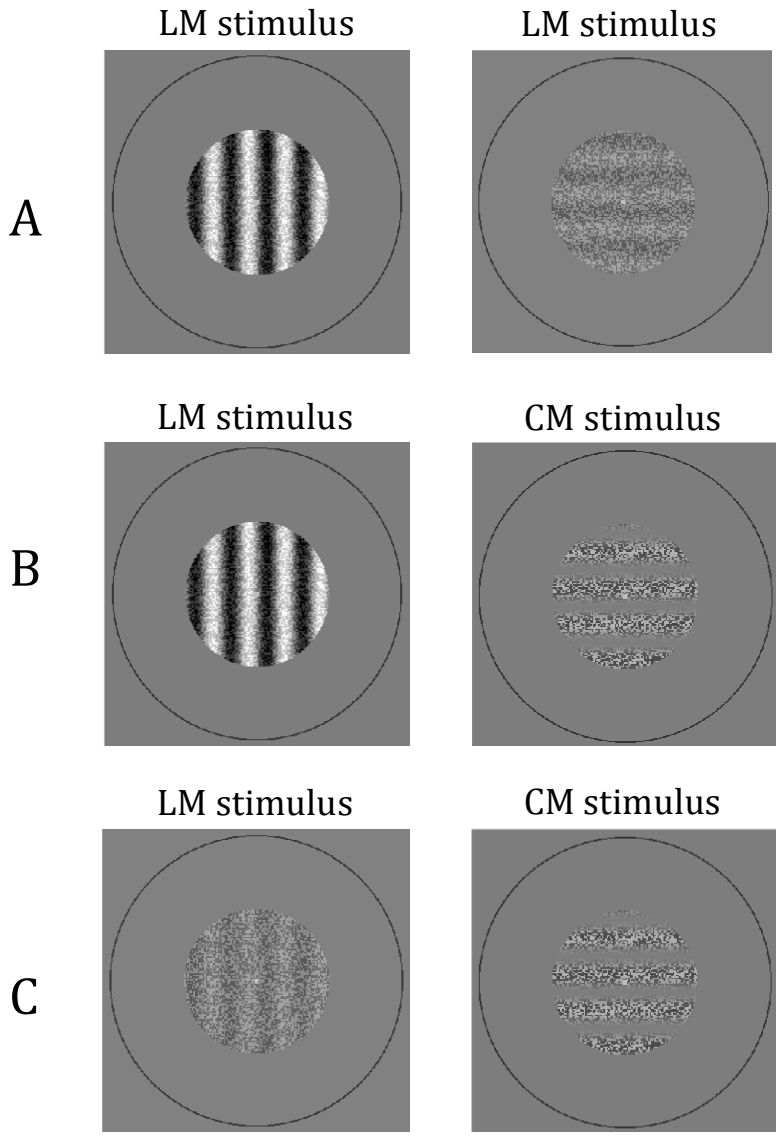

Figure 4.1: Demonstration of binocular rivalry using LM stimuli only and between LM and CM stimuli. The reader is encouraged to free-fuse the pairs of stimuli to experience binocular rivalry. A) Orthogonally orientated high- and low-contrast LM gratings. The high-contrast grating will be predominately visible during binocular rivalry. B) The same high-contrast LM grating competes with a CM grating for predominance. Exclusive visibility of the high-contrast LM grating should be lower than in A) and similar to that generated by the CM grating (based on the results of the current chapter). C) A low-contrast LM grating competes with the same CM grating. Both gratings are of approximately equal visibility. The CM grating dominates perception. Both stimuli were surrounded by a fusion lock 4 deg in diameter, and contained a static fixation spot (size of 6x6 pixels) in the centre with a luminance contrast of 0.20.

All stimuli were circular with a diameter of 2 deg and contained a 2 c/deg sinusoidal grating (Figure 4.1). A LM grating was presented to one eye and an orthogonally orientated CM grating to the other eye. LM gratings were presented at contrasts of 0.04, 0.10, 0.20, 0.40 and 0.78, which correspond to visibility levels of 2x (± 0.95 indicating ± 1 SEM), 5x (± 0.83), 11x (± 1.66), 22x (± 3.33) and 43x (± 6.49), respectively, measured according to a previous protocol (see Section *2.5.1 Methods*). The modulation of the CM grating was fixed at 1.00 resulting in a visibility level of 7x (± 0.96) (see Appendix *6.3 Luminance profiles for LM and CM stimuli*). The stimuli were presented on a grey background with a mean luminance of 49.8 cd/m^2.

An experiment for one participant comprised two sessions, each carried out on separate days. A session included twenty trials, each lasting at least 120 s. The experimental order of a session was counterbalanced in respect to grating orientation, LM contrast, stimulus type-to-eye relation. Instructions and practice trials were given before the data collection of the experiment started. Breaks in-between trials were permitted. A complete session lasted between 45 and 60 min, depending on the breaks for each participant.

4.2.3 Procedure

The procedure was identical to that described in the third chapter (see Section *3.2.3 Procedure*).

4.2.4 Data analysis

The same perceptual states and change categories were analysed as described in the third chapter (see Section *3.2.4 Data analysis*).

The trial duration in this study was 120 s, the same as the trial duration of the first study (*Chapter 2*). Thus, the data of this chapter can be compared with data gained in the first study, in which a CM grating competed with an orthogonal CM grating, and a LM grating with an orthogonal LM grating.

4.2.4.1 Analysis of perceptual phase distributions

The distributions of the exclusively visible, piecemeal and superimposed perceptual phase durations were analysed in the same way as described in Section *3.2.4.1 Analysis of perceptual phase distributions*.

4.3 Results

4.3.1 Perceptual states and mean durations

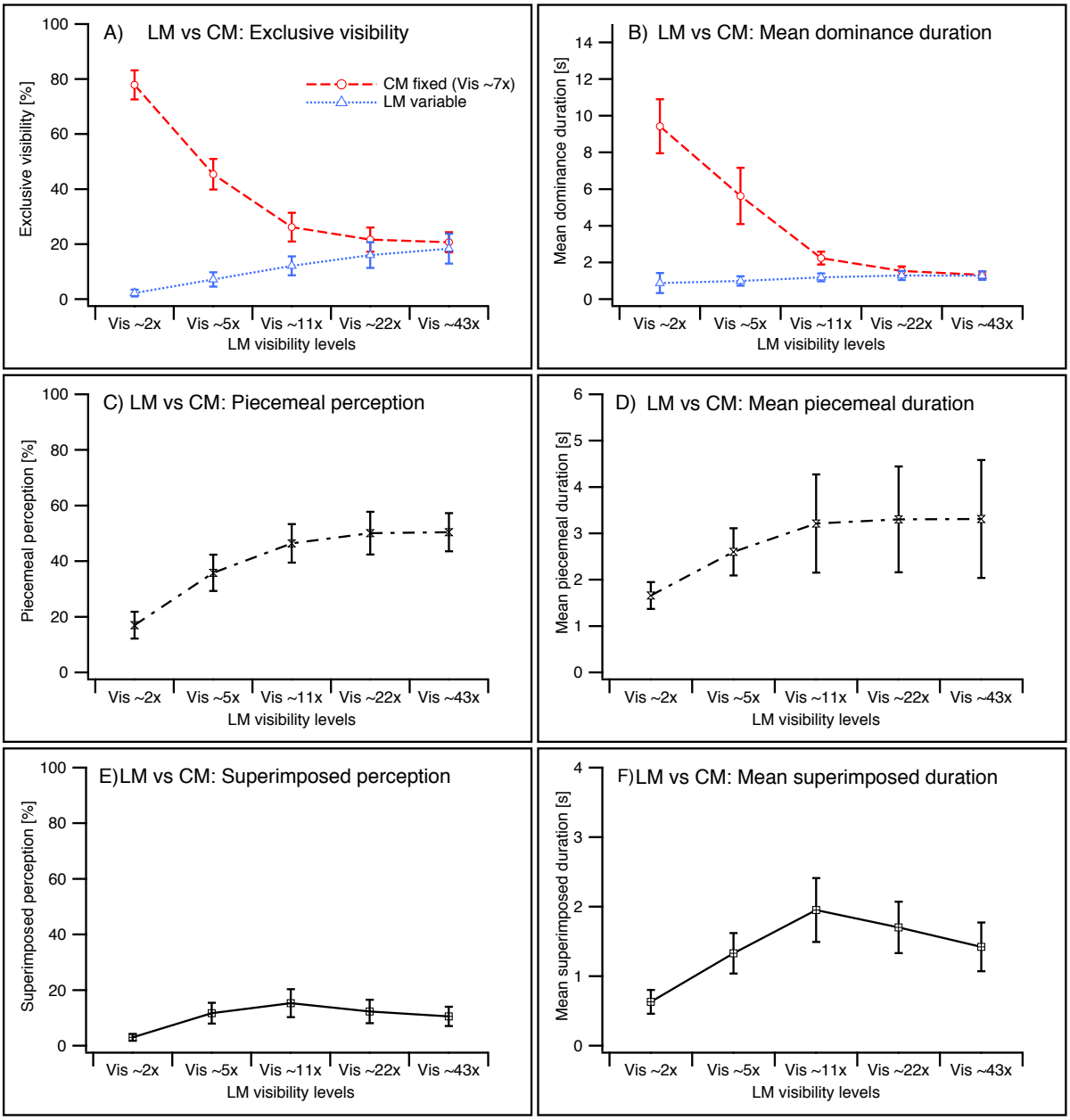

Figure 4.2: Results for the perceptual states and their respective mean durations, averaged across participants and trials, for competing CM and LM gratings. The contrast-modulation depth of the CM grating was fixed whereas the LM stimulus contrast varied. The visibility levels are shown in the legend and along the x- axis for CM and LM stimuli, respectively. A) Relative exclusive visibilities for CM (red circles connected by a dashed line) and LM stimuli (blue triangles connected by a dotted line). C) Piecemeal perception (grey hourglasses connected by dash-dotted line). E) Superimposed perception (black boxes connected by a solid line) as well as their mean durations B), D), F), respectively. Error bars indicate ± 1 standard error.

The relative proportions of exclusive visibility, piecemeal and superimposed percepts, averaged across trials and observers, are depicted in Figure 4.2 A, C and E, respectively. I aim to investigate the effects of stimulus type and LM visibility on the characteristics of binocular rivalry and describe as well as statistically analyse these results for each perceptual state separately.

A LM grating and an orthogonally orientated CM grating do engage in binocular rivalry (Figure 4.2A). The most outstanding result of this first experiment is that exclusive visibility (i.e., the proportion of time when only one grating was visible) of the LM stimulus was never greater than the exclusive visibility of the CM stimulus (Figure 4.2A). As the visibility of the LM stimulus increased, its exclusive visibility also increased and that of the CM grating decreased. This results in a statistically significant interaction between the effects of stimulus type and visibility of the LM grating [$F(1.6, 14.8) = 55.4$, $p < 0.001$] on exclusive visibility. Even when the visibility of the LM grating was much higher (~ 43x) than that of the CM one (~ 7x), exclusive visibility was similar and not significantly different [planned comparison, $p > 0.05$] at 20.7 ± 3.7 (standard error) % for the CM and 18.4 ± 5.4 % for the LM grating. When the two stimuli were presented at similar visibility levels (CM ~ 7x and LM ~ 5x), exclusive visibility was significantly greater [planned comparison, $p < 0.001$] for the CM (44.1 ± 5.4 %) than the LM (7.1 ± 2.7 %) grating.

Piecemeal perception (Figure 4.2C) decreased when the visibility of the LM stimulus decreased [$F(1.3, 11.5) = 16.6$, $p < 0.01$]. Superimposed perception (Figure 4.2E) occurred much less frequently (3.2 - 15.2 %) and reduced as the visibility of the LM grating changed from ~ 11x to ~ 2 x, but this effect did not reach statistical significance [$F(2.2, 19.7) = 3.5$, $p = 0.05$].

Figure 4.2B, D and F show the respective mean durations. The mean durations show similar trends and statistical outcomes as the relative proportions of percepts, reported above.

In conclusion, highly visible LM stimuli never generated significantly greater proportions or longer phases of exclusive visibility than CM stimuli with a lower visibility. When the visibility of the LM stimulus was lowered, CM stimuli showed significantly greater proportions and longer phases of exclusive visibility. The proportions and length of phases for

piecemeal perception decreased when the visibility of the LM grating decreased whereas superimposition occurred rarely.

4.3.2 Perceptual changes and reversions

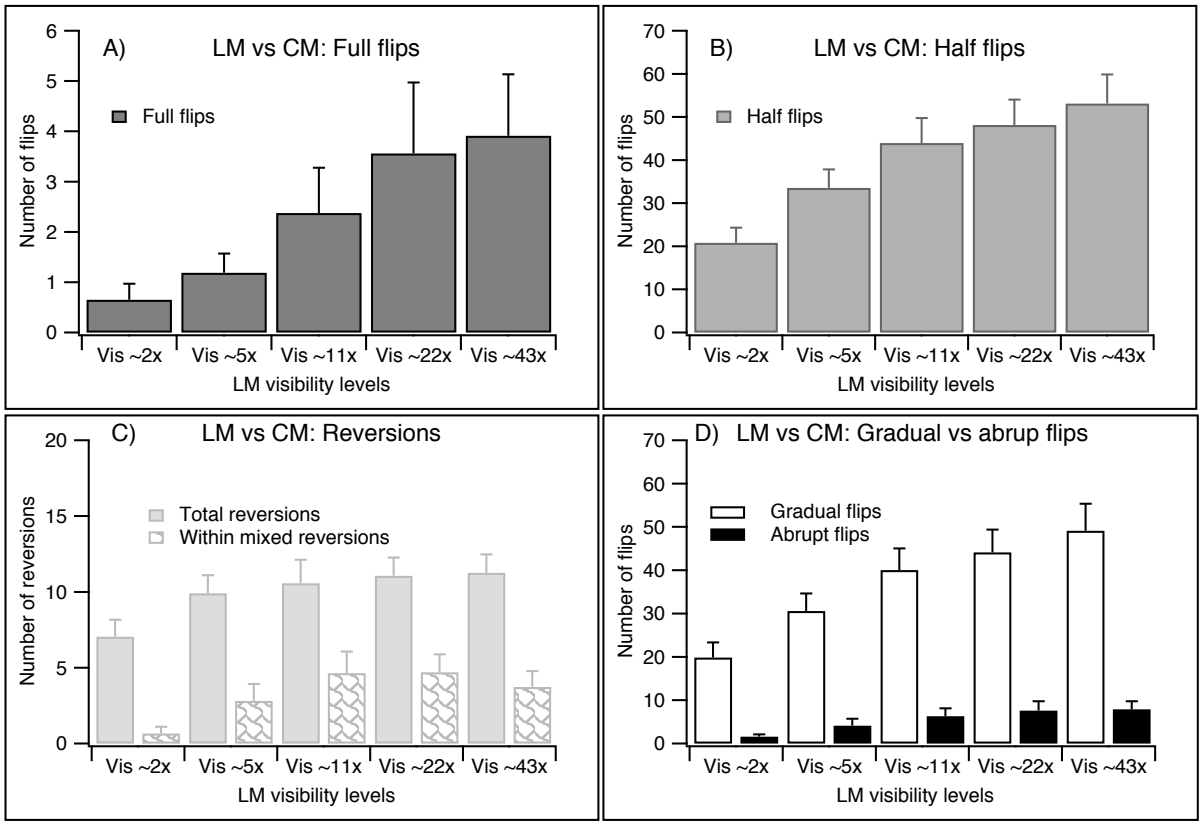

Figure 4.3: Results for orthogonally presented CM and LM stimuli, averaged across trials and participants, for total number of full flips (dark-grey bars)(A), half flips (medium-grey bars) (B), reversions (light-grey bars) and reversions within mixed states (scaled grey bars) (C), and gradual (white bars) versus abrupt (black bars) flips (D). Error bars indicate + 1 standard error.

Figure 4.3A-D represents perceptual changes and reversions, averaged across participants and trials. The most notable result is the frequent alternation (Figure 4.3A) between a highly visible LM stimulus (visibility ~ 43x) and a much less visible CM stimulus (visibility ~ 7x). As the visibility of the LM grating was reduced, there was a statistically significant reduction in all perceptual changes and reversions (Table 4.1). Half flips occur more often than full flips and gradual flips occur more often than abrupt flips under all stimulus conditions.

Perceptual change categories	Variable: Visibility
Full flips	[$F(1.4, 12.3) = 5.8, p < 0.05$]
Half flips	[$F(2.2, 19.5) = 21.9, p < 0.001$]
Reversions	[$F(3.1, 27.5) = 8.2, p < 0.001$]
Within mixed reversions	[$F(2.2, 19.6) = 4.5, p < 0.05$]
Gradual flips	[$F(2.2, 19.5) = 19.6, p < 0.001$]
Abrupt flips	[$F(1.9, 17.1) = 19.6, p < 0.01$]

Table 4.1: Statistical results for perceptual changes of the third experiment.

4.3.3 Perception across time

Figure 4.4 shows the effects across time on exclusive visibility for CM and LM stimuli, piecemeal, and superimposed perception, averaged and analysed across participants and trial time, in 3-s intervals for various LM visibility levels. As a trial consisted forty '3-s-bins', effects between single '3-s-bins' might be not revealed with an ANOVA testing small effects across time. In fact, such effects have been found in the second and third chapter (see Section *2.5.3 Results* and *3.3.3 Results of perception across time*). Hence, I also planned comparisons to analyse differences between single '3-s-bins'.

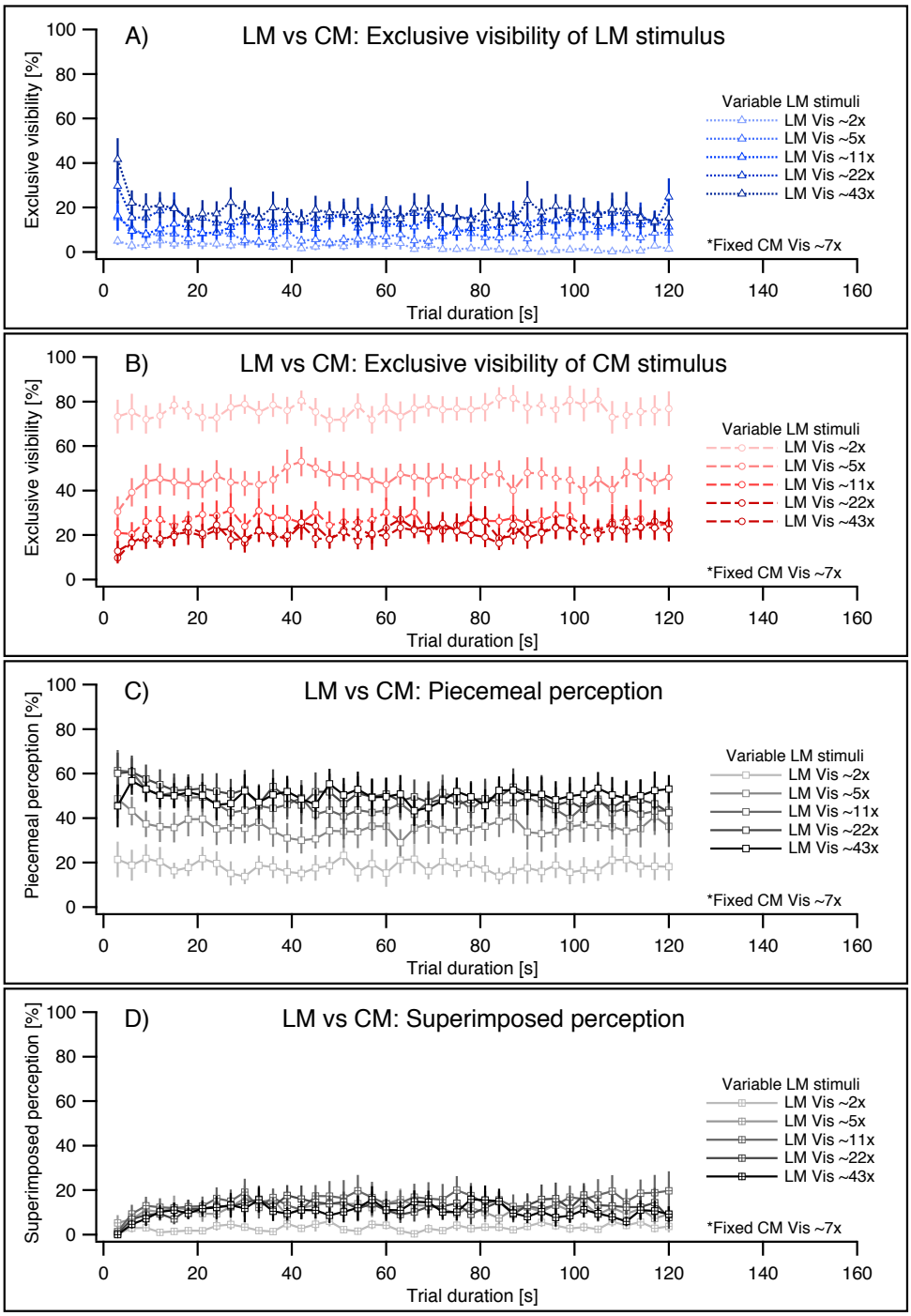

Figure 4.4: Analysis of perceptual states across time, averaged across trials and participants, and calculated every 3 s ('3-s-bin') across 120 s for exclusive visible LM stimuli (blue dotted lines with triangles) and exclusive visible CM (red dashed lines with circles), piecemeal perception (grey solid lines with empty squares) and superimposed perception (grey solid lines with grid squares). The various hues within each graph represent different LM visibility levels, e.g. a black solid line in graph D) represents superimposition generated by LM visibility ~ 43x condition whereas the lightest grey solid line indicates superimposition for the LM visibility ~ 2x condition. Error bars indicate ± 1 standard error.

There was a mild, but significant change of exclusive visibility of the LM grating across trial duration [$F(3.5, 31.6) = 3.1$, $p < 0.05$] (Figure 4.4A). A mild trend of decreasing LM's exclusive visibility during the first 6 s was not significant [planned comparison $p > 0.05$]. Exclusive visibility of CM stimuli (Figure 4.4B) showed no main effect across trial duration [$F(7, 62.5) = 1.8$, $p > 0.05$]. A planned comparison confirmed also that for CM stimulus' exclusive visibility does not change significantly during the first 6 s [$p > 0.05$].

Piecemeal perception (Figure 4.4C) did not change significantly across trial duration [$F(4, 35.7) = 1.9$, $p > 0.05$] and also not during the first 6 s [$p > 0.05$]. Superimposed perception (Figure 4.4D) increases significantly across trial duration [$F(3.3, 30.1) = 3$, $p < 0.05$], which was accompanied by an increase of superimposition during the first 6 s [planned comparison $p > 0.05$] except when visibility of the LM stimulus was ~ 2x and ~ 5x above detection threshold.

4.3.4 Distribution of perceptual phases

Exclusively visible CM percepts occurred more often than LM percepts (Figure 4.5, top). The reduction of visibility of the LM grating decreased the number of exclusive and piecemeal events, as well as superimposed events near-threshold conditions (visibility ~ 5x and ~ 2x). Piecemeal and superimposed events also demonstrated the typical gamma distribution shape (Figure 4.5 middle and bottom panels, respectively). Whilst gamma functions fit to distributions of piecemeal percepts were little influenced by changes in the visibility of the LM grating, the fits for the distributions of superimposition were poorer when the LM grating was near-threshold than at higher visibility levels.

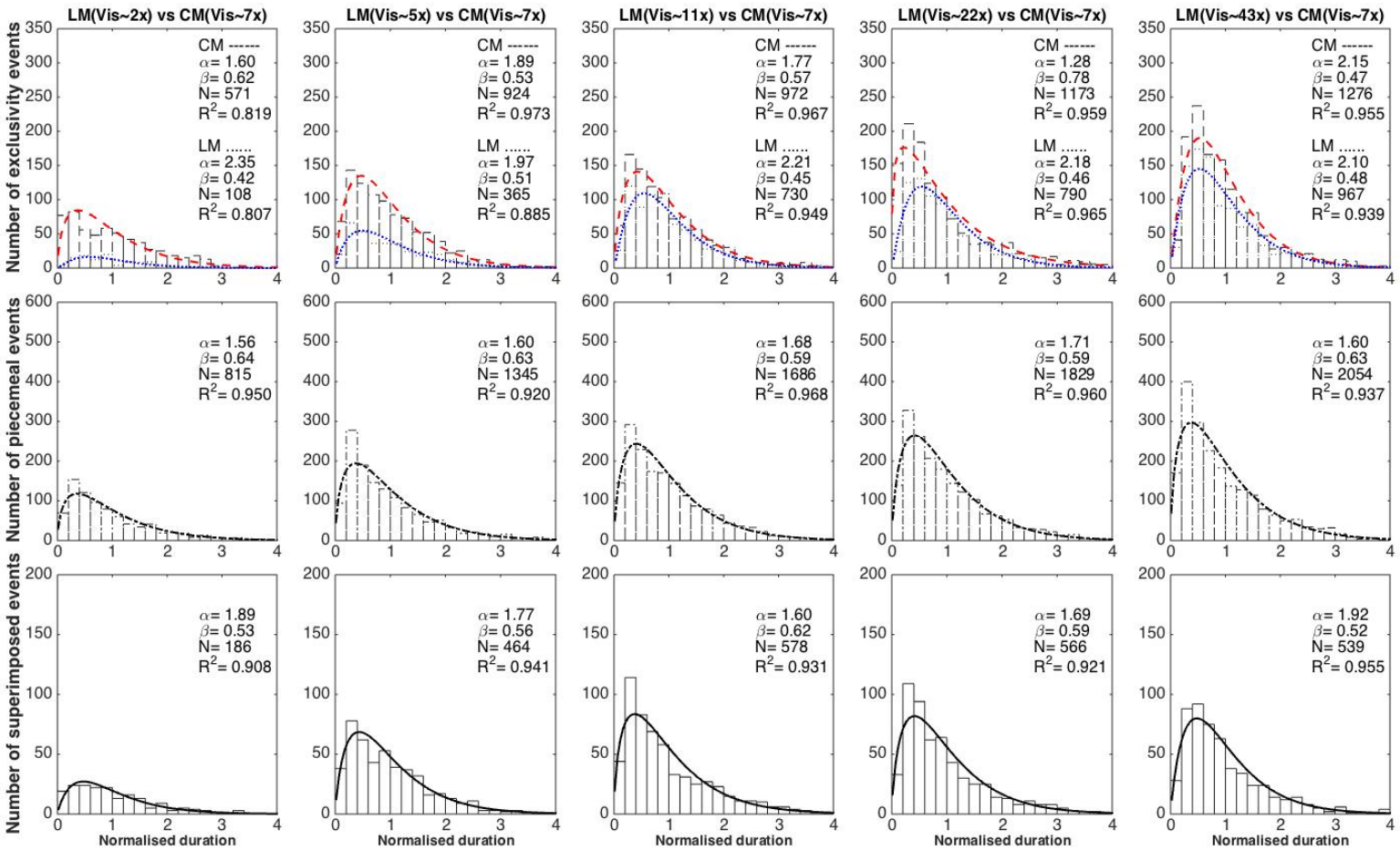

Figure 4.5: Multi-plot representing distributions of LM and CM exclusively visible, piecemeal and superimposed percepts, fit with a gamma function. The graphs on the top represent LM (blue dotted lines) and CM (red dashed lines) gamma distributions for exclusive visibility. The middle and bottom rows show gamma distributions for piecemeal (black dotted-dashed lines) and superimposed perception (black solid lines), respectively. The x-axes represent the frequencies of perceptual events. The y-axes depict normalised period durations. The normalisation was achieved by dividing the durations of the individual events by the relevant mean duration. α is the 'shape' parameter, β is the 'scale' parameter, N is the total number of events.

4.4 LM versus CM stimulus: An experiment concerning Levelt's modified fourth law

The first experiment of this chapter examined the characteristics of binocular rivalry when a LM and a CM stimulus compete. Changes in visibility of the LM grating also allow the results of that experiment to be considered in relation to Levelt's modified first, second, and third laws, which make predictions based on unilateral changes in visibility levels. An additional experiment was carried out to test the influence of bilateral changes in visibility on the characteristics of binocular rivalry when a LM and a CM stimulus compete to address Levelt's modified fourth law.

4.4.1 Methods

Five adults (3 male) participated. The task and procedure were the same as in the first experiment of this chapter.

4.4.1.1 Stimuli and analysis

To test Levelt's modified fourth law, visibility levels of both gratings were set to be equal at ~3.5x, ~ 5x or ~ 7x detection threshold. Luminance-modulations of 0.07, 0.10, 0.14 and contrast-modulations of 0.50, 0.70, 1.00 were used for LM and CM stimuli, respectively, to achieve the required levels. The experiment was carried out in one day and included 8 trials per LM/CM combination, resulting in 24 trials in total. The experimental order of a session was counterbalanced in respect of grating orientation, visibility, stimulus type-to-eye relation. The experiment took around 60 minutes, depending on the breaks of the participant needed between trials. All other stimuli properties were as in the first experiment of this chapter. Only the full flip rate was calculated and then averaged across trials and participants because the rate of full flips represents the alternation rate in Levelt's fourth law, which is defined as an abrupt change from one exclusively visible percept to the other.

4.4.2 Results

Full flips were almost (Figure 4.6H) absent and did not change significantly with a change in visibility of the rivalling gratings [$F(0.1, 0.4) = 1.3$, $p > 0.05$]. The results therefore do not follow Levelt's modified fourth law, which predicts an increase in full flip rate with an increase in bilateral visibility.

4.4.3 Predictions based on Levelt's modified four laws compared with the 'LM versus CM' results

Figure 4.6 compares the results of the first and second experiment of this chapter with predictions made on the basis of Levelt's modified laws (Brascamp, Klink and Levelt, 2015). The results of the first experiment are replicated in Figure 4.6 B, D, and F whereas Figure 4.6H shows the result of the second experiment concerning Levelt's modified fourth law (see Section *4.4 LM versus CM: An experiment concerning Levelt's modified fourth law*).

Levelt's modified first law predicts that the exclusive visibility of a highly visible stimulus predominates perception and that when the visibility levels are equal, exclusive visibility of the two rivalling stimuli should be comparable (Figure 4.6A). The results of the first experiment (Figure 4.6B) do not follow the predicted result: exclusive visibility of the CM and LM grating was not significantly different when a highly visible LM stimulus (~ 43x) competed with a CM stimulus of lower visibility (~ 7x) whereas when the two were of similar visibility, the CM stimulus generated greater proportions of exclusive visibility than the LM stimulus.

The modified second law predicts that the mean exclusivity duration of the stronger stimulus will increase as the difference in visibility between the rival stimuli increases whereas the mean exclusivity duration of the weaker stimulus will slightly decrease (Figure 4.6C). As for the first law, the results of the current experimental chapter indicate a different pattern. When the difference in visibility levels between the LM and CM was greatest (visibility ~ 43x and visibility ~ 7x, respectively), the mean exclusivity durations were not significantly different whereas the difference increased with decreasing visibility of the LM grating (Figure 4.6D). On the other hand, mean exclusivity duration of the LM stimulus did indeed decrease, as predicted, when its visibility level was reduced.

The modified third law predicts that the full flip rate should be highest when visibility levels of two rival stimuli are the same and that it should reduce as the difference between the visibility levels increases (Figure 4.6E). Again, the actual results indicate the opposite pattern: full flips occurred most often when the difference in visibility levels between the LM and CM stimulus was greatest (Figure 4.6F).

The modified fourth law suggests that an increase of full flips should occur when a) both visibility levels are the same and b) when the level of visibility of both stimuli is increased (Figure 4.6G). The results of the second experiment in this chapter showed that an increase visibility, whilst keeping it equal for the two stimuli, did not significantly increase the full flip rate (Figure 4.6H).

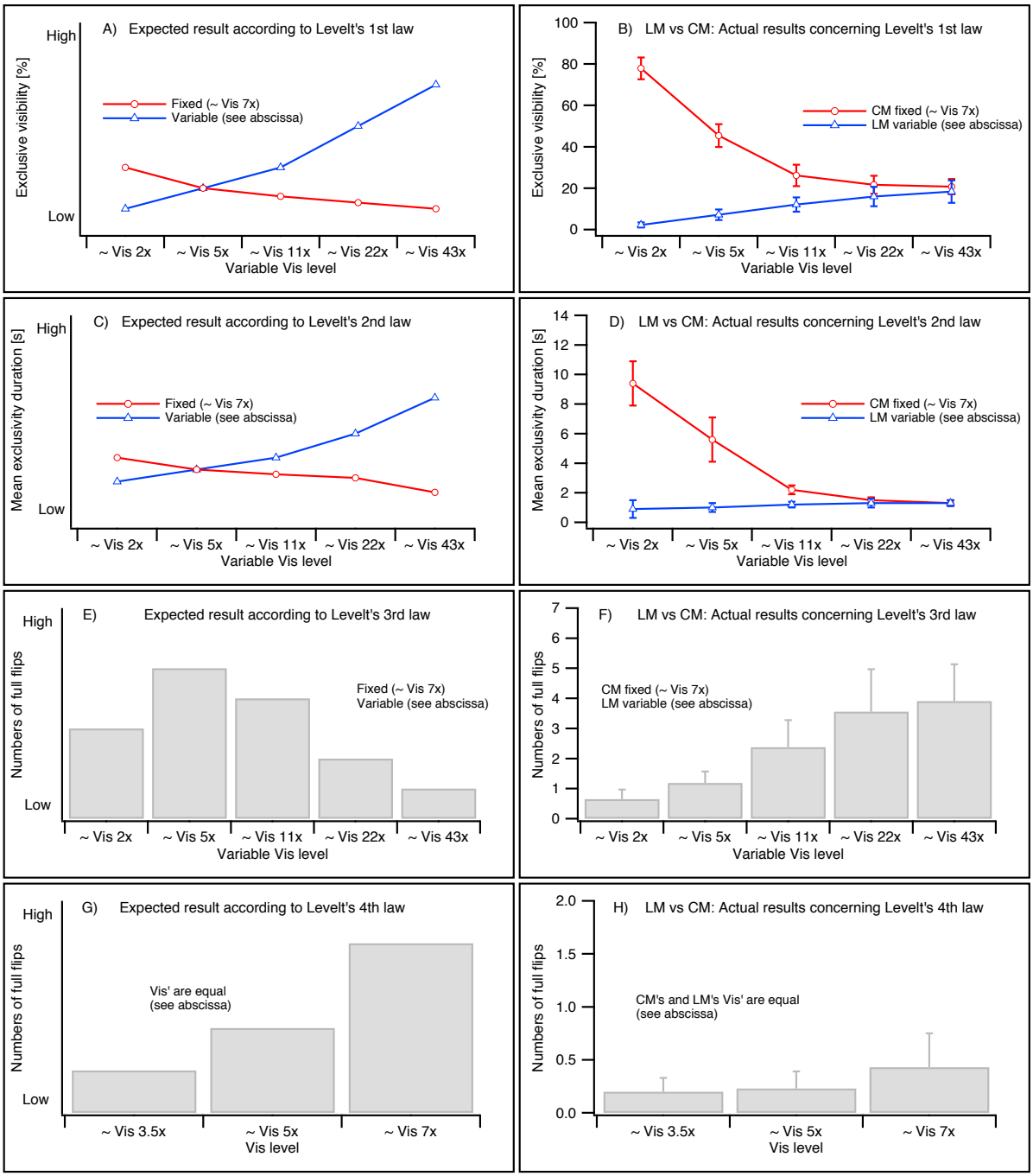

Figure 4.6: Comparison of Levelt's four laws and the results of the current study. Visibility served as metric to indicate stimuli strengths. The left graphs indicate the expected results following Levelt's modified laws; the right graphs depict the actual results. Vertical bars represent +1 standard error.

4.5 CM versus CM: Do Levelt's modified four laws hold when only CM stimuli compete?

So far I have demonstrated that Levelt's modified laws do not hold if a LM stimulus competes with CM stimulus under binocular rivalry conditions (Figure 4.6). However, it is unknown whether rivalrous CM stimuli generally do not follow Levelt's modified laws or whether the findings of the previous two experiments in this chapter are the result of different stimulus types, which compete with each other. Therefore, I conducted an additional experiment to address this question.

4.5.1 Methods

Ten adults (4 female), including six participants from the first experiment, of an average age of 26 ± 6.2 years participated. The task and procedure were the same as in the first experiment of this chapter.

4.5.1.1 Stimuli and analysis

I conducted an experiment to test whether Levelt's modified four laws hold when only CM stimuli competed and compared those results with predictions based on Levelt's modified four laws (Brascamp, Klink and Levelt, 2015) as well as with results of comparably visible LM stimuli. To clarify, in this experiment the two orthogonal gratings were of the same type; either LM versus LM or CM versus CM.

For both stimulus types, the visibility of one grating was fixed at 3.5 x detection threshold whilst the visibility of the other grating was ~2x, ~3.5x or ~7x. These levels were generated by the following modulations: for the LM gratings, the fixed modulation was 0.07 whilst the variable ones were 0.04, 0.07 and 0.14; for the CM gratings, fixed modulation was 0.50 whereas the variable modulations were 0.28, 0.50 and 1.00. The superimposition results for LM and CM stimuli visibility of ~5x and ~7x, respectively, were taken from the third chapter (see Section *3.3.1 Perceptual states and mean durations*).

The experiment was carried out in two sessions on separate days. A session included 24 trials. The experimental order of a session was counterbalanced in respect of grating orientation, visibility and stimulus type. A session took approximately 60 minutes, depending on the breaks of the participant between trials. All other stimulus properties were as in the first experiment of this chapter. The proportions of exclusive visibility for each stimulus, their respective mean durations and the full flip rate were calculated and then averaged across trials and participants as measures for the first three laws.

For the analysis of the modified fourth law, I compared the result (for LM and CM) of full flip rates when both gratings were presented at the same visibility of ~ 3.5x with findings from a previous experimental chapter (see Section *2.5.3 Results*), in which binocular rivalry was initiated with LM stimuli using a visibility level ~ 22x and CM gratings with visibility levels of ~ 7x. All other stimulus properties were the same as described in the second experimental chapter.

4.5.2 Results: CM versus CM and LM versus LM in the light of Levelt's modified laws

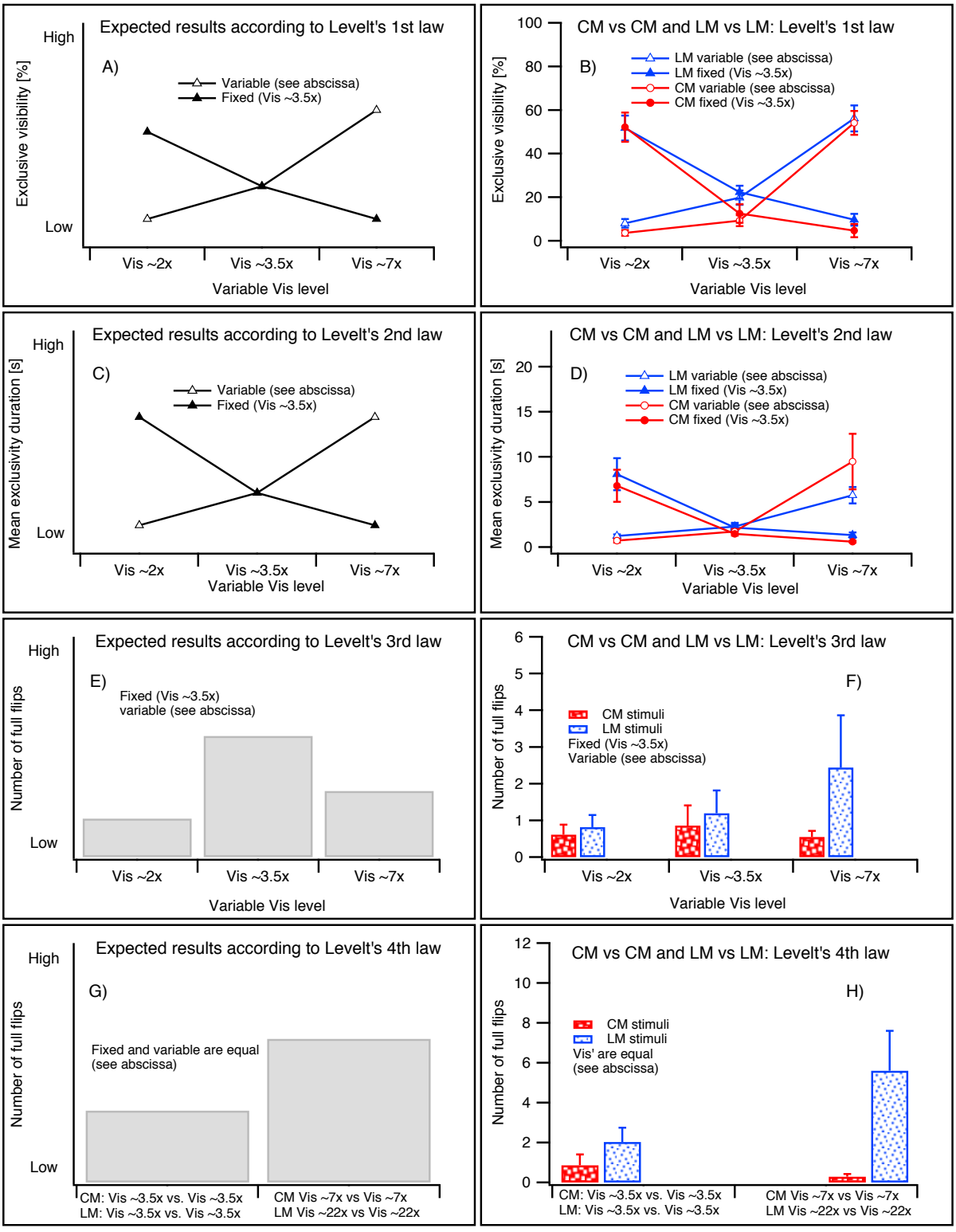

Figure 4.7: Comparison of expected findings according to Levelt's modified four laws (left column) with the results of the current experiment (right column). Visibility levels served as metrics to indicate stimulus strengths (x-axes). Vertical bars represent +1 standard error.

Levelt's modified first law predicts that the stimulus with the higher visibility will predominate perception whereas when visibility levels of the rival stimuli are equal, the proportions of exclusive visibility of the two stimuli should be similar (Figure 4.7A). The results for LM and CM stimuli follow the predicted pattern (Figure 4.7B) and are therefore fully in line with Levelt's modified first law.

The modified second law predicts that an increase in the difference in visibility levels between the two stimuli will primarily increase the mean exclusivity duration of the stimulus with the higher visibility (Figure 4.7C). This can be seen in the results for both LM and CM stimuli shown in Figure 4.7D.

Levelt's modified third law addresses the full flip rate: the increase of the visibility differences will reduce the full flip rate, which implies a peak full flip rate when the visibility levels between the stimuli are equal (Figure 4.7E). The CM stimuli show a mild trend towards the expected result, whereas LM stimuli's results increase with increasing variables visibility.

Finally, Levelt's modified fourth law predicts the increase of the full flip rate when visibility levels of both stimuli are equally increased, but this effect may reverse for near-threshold stimuli (Figure 4.7G). The full flip rate for LM stimuli increases with an increase in visibility level (from 2.0 ± 0.7 to 4.2 ± 1.3 full flips), but was little changed for CM stimulus conditions (0.9 ± 0.5 to 0.3 ± 0.1 full flips). The law therefore holds only for competing LM stimuli.

4.5.2.1 CM versus CM and LM versus LM: Results for superimposed perception

The results show that when two CM gratings compete, only Levelt's modified first and second laws hold, whereas all four modified laws hold for LM stimuli. The third and fourth law describe the effects of changes in visibility on alternation rates. CM stimuli may not replicate results in line with those two laws as they may engage in binocular combination before they alternate rather than abruptly change from one exclusive state to the other. Hence, I compared LM and CM stimuli's results for superimposition when the visibility level was either unilaterally or bilaterally changed (see Section *4.6 CM versus CM: Do Levelt's modified laws hold when only CM stimuli compete?*).

Regardless of the differences in visibility levels between the two rivalrous stimuli, greater proportions of superimposition (Figure 4.8A) [$F(1, 9) = 10.8$, $p < 0.01$] and longer mean durations (Figure 4.8B) [$F(1, 9) = 9.2$, $p < 0.05$] were found for CM than for LM stimuli. Also, greater proportions of superimposition occurred when the visibility levels of the two stimuli were equal (Figure 4.8A) than when they were different resulting is a statistically significant effect of interocular differences in visibility on superimposition [$F(1.4, 12.3) = 6.7$, $p < 0.05$].

A bilateral increase of visibility levels increased the proportion of superimposition for CM stimuli but had no effect on LM stimuli (Figure 4.8C). This leads to a statistically significant interaction between stimulus type and visibility level [$F(1, 14) = 52.9$, $p < 0.001$]. Superimposition generated by CM stimuli tended to increase when the visibility levels were bilaterally increased, even though this trend was not statistically significant [planned comparison, $p > 0.05$].

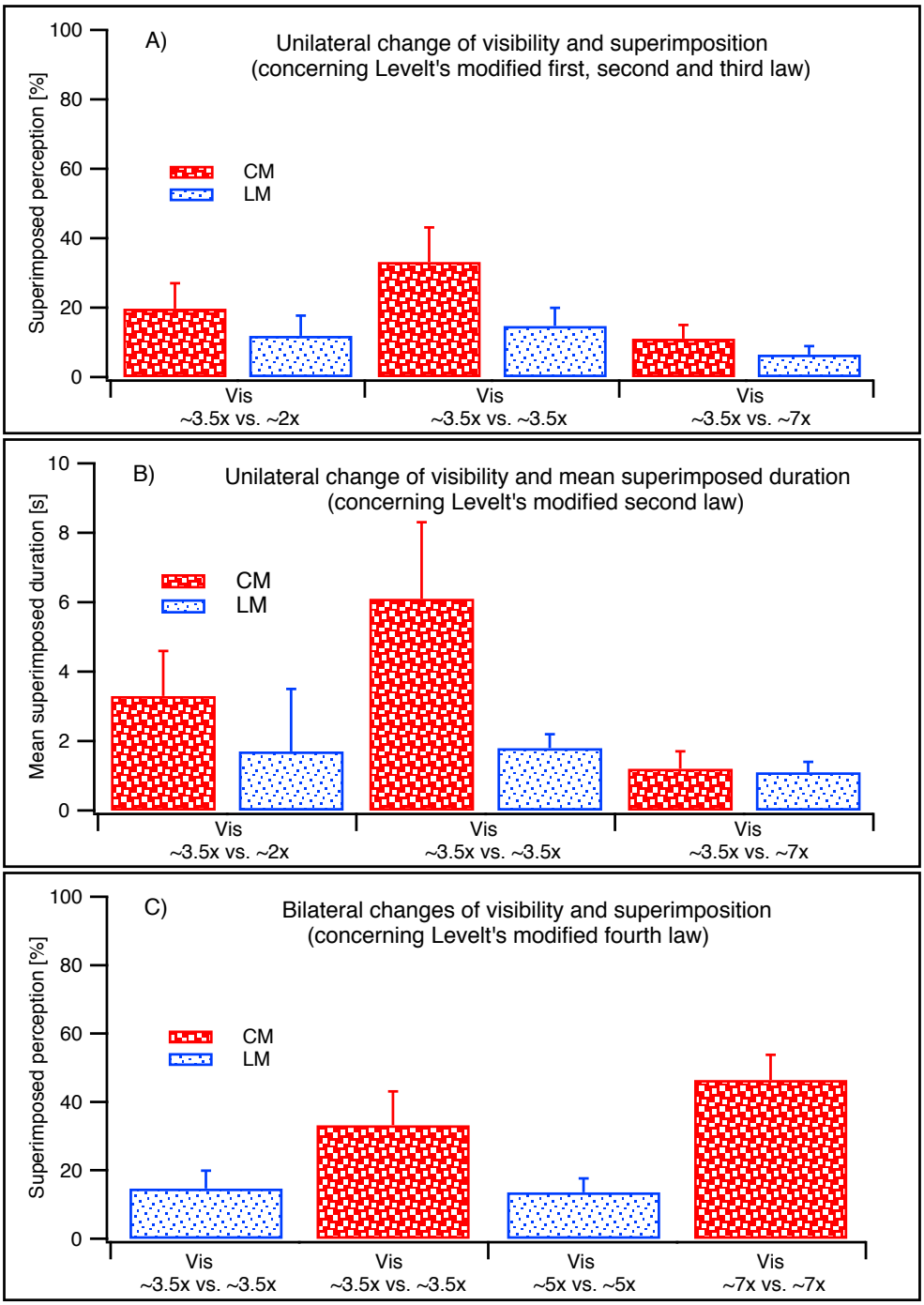

Figure 4.8: The influence of visibility level changes on the proportions of superimposition for LM and CM stimuli. The red bars with big dots represent results for CM stimuli whereas the blue bars with small dots show results for LM stimuli. A) Relative proportions of superimposed perception when visibility level changes unilaterally. B) Mean superimposed duration when visibility level changes unilaterally. C) Relative proportions of superimposed perception when visibility level increases bilaterally.

4.6 Discussion

The experiments in this chapter tested several LM and CM binocular rivalry conditions. The results demonstrated that a LM grating does engage in binocular rivalry with an orthogonally orientated CM one, but visibility levels of the stimuli do not predict the outcomes of this competition as described by Levelt's modified laws. The results also revealed that Levelt's modified four laws only hold for a limited range of stimulus type conditions (Table 4.1). The following discussion shall address main findings as well as discuss implications of the results for the processing during LM and CM binocular rivalry, which will ultimately lead to a model of those stimulus types.

4.6.1 A model for LM and CM binocular rivalry

Why did LM stimuli not reach predominance when competing with CM stimuli, even when the highest luminance contrast was used (Figure 4.2A)? It has been suggested that binocular rivalry is mediated by a mutual inhibition mechanism (e.g. Blake, 1989; Seely and Chow, 2011), which leads to dominance of one monocular percept and alternation of this percept with the other monocular percept across trial time. Models concerning mutual inhibition have assumed that mainly monocular units compete for predominance whilst receiving feedback and from higher cortical areas (e.g. Tong et al., 2006). Unlike luminance-defined stimuli (used in previous studies on binocular rivalry), CM stimuli are suggested to be processed in multiple stages (e.g. Schofield and Georgeson, 1999; Baker and Mareschal, 2001), beginning with an orientation- and spatial-frequency-selective response to luminance in a first stage. After rectification of the first stage, the output is passed to a second stage, which gives selective responses to variations of the first stage outputs and represents these variations across regions of the CM stimulus. In particular, this second stage has been recently suggested to initially process input from both eyes, i.e., it is involved in binocular processing (e.g. Hairol and Waugh, 2010; Chima et al., 2015; see also Wong et al., 2001). Previous investigations of CM binocular rivalry support this view as I found that rivalrous CM stimuli generate significantly more superimposed percepts than comparable LM stimuli (see *Chapter 3*).

In Figure 4.9, I present a model, which addresses the different binocular rivalry characteristics for LM, CM, and LM versus CM binocular rivalry. If binocular rivalry is initiated by orthogonally orientated high contrast gratings, then monocular neurones of one eye are active and generate the percept of this eye whilst at the same time, the neurones of the other eye are suppressed either completely (exclusive visibility) or locally (piecemeal percepts) (Figure 4.9A). When rival LM gratings are near-threshold levels, superimposition arises (see for L stimuli Brascamp et al., 2006; Liu et al., 1992) and is likely to be the result of involvement of binocular in the perceptual processing (Figure 4.9B). As mentioned earlier, CM stimuli are likely to require additional computation, well described in filter-rectify-filter models (e.g. Baker and Mareschal, 2001; Landy and Graham, 2004). Under interocularly correlated noise condition, I suggested previously that the noise-carriers of CM stimuli do not engage in binocular rivalry alternation since the corresponding interocular luminance information is identical (see *Chapter 2*). The competition arises instead between orientation-selective neurones, which encode the envelope (Figure 4.9). I speculate that extrastriate areas V01, V2 and even V3 are potential candidates for the additional processing as they have been identified as sensitive to second-order envelope information in both animals (single-cell studies e.g. Li et al., 2014b; Tanaka and Ohzawa, 2006) and humans (neuro-imaging study (Larsson, Landy and Heeger, 2006)). In the first experiment of this chapter, I have demonstrated that CM stimuli can provoke perceptual alternations if they compete with highly visible LM stimuli (Figure 4.3). As Figure 4.9D depicts, mutual inhibition arises between the first filter stage of the CM stimulus and the LM stimulus as well as a feedback signal from the second filter stage, which additionally suppresses the LM stimulus. In fact, the involvement of binocular units may encourage the visual system to suppress the monocular first-order input from the LM stimulus via feedback signals. The LM stimulus mutually inhibits only with the first-order noise stage of the CM stimulus whereas the feedback signal from the second-order envelope stage is constant. Consequently, reducing the visibility of the LM stimulus to a reduction of mutual inhibition between the first-order component of the LM and CM grating, which ultimately generates a predomination of the CM stimulus.

There is an ongoing debate of whether binocular rivalry is a product of competition between the neurones early in the visual cortex or whether neurones that receive input from both eyes mediate competition between the pattern in later stages of visual processing, or perhaps a combination of both (e.g. von Helmholtz, 1867; Blake, 1989; Blake and Logothetis, 2002; Tong et al., 2006). Results of neuro-imaging studies have shown that alternation of exclusive

percepts under conventional binocular rivalry conditions correlates with alternation of metabolic activity as early as V1 (Tong and Engel, 2001; Lee and Blake, 2002) or even LGN (Wunderlich et al., 2005; Haynes et al., 2005). Also, meaningful stimuli (e.g. faces and house) show neural correlates during binocular rivalry dominance phases as early as V1 (Lee and Blake, 2002) and gratings even in lateral geniculate nucleus (LGN) (Wunderlich et al., 2005; Haynes et al., 2005). On the other hand, results in single cell studies in animals have challenged the view of an early processing site for exclusivity since rivalry evoked only a few neurones in early visual cortex, but more in later, more binocular regions (Logothetis, 1998a).

My model suggests that several processing areas must be involved during binocular rivalry of LM and CM stimuli. Monocular neurones process exclusive visibility of LM stimuli whereas CM exclusivity comprises additional neuronal columns, which process the envelope information at a binocular stage (Figure 4.9). The mixed states are likely to involve binocular processing areas. The piecemeal perception is thought to be binocular rivalry in local zones across the visual field (Blake et al., 1992), which would mean that the processing sites of exclusively visible and piecemeal percepts are identical, however, some results of neuro-imaging studies revealed that transition phases (likely to be piecemeal percepts) generate metabolic activity in later visual areas of the brain, but did not lead to significantly changes of activity in V1 (Lumer et al., 1998; Lumer and Rees, 1999; Polonsky et al., 2000). On the other hand, Lee, Blake, and Heeger (2005) observed an increase and a decrease of metabolic activity in V1 that corresponded with the perceptual wave-like transition between low and high-contrast annulus gratings. Hence, I suggest that piecemeal perception for both LM and CM stimuli might have a monocular processing site with potential feedback signals from higher cortical areas due to visual attention (Scocchia, Valsecchi, and Triesch, 2014). Superimposition during binocular rivalry was thought to be an indicator for binocular fusion (e.g. Liu et al., 1992; Brascamp et al., 2006; Klink, Brascamp, Blake, and van Wezel, 2010; Klink, Brascamp, Blake, and Wezel, 2010). Thus, I assume that superimposition involves binocular neurones, which combine information rather than engage in interocular competition. In conclusion, my proposed model suggests that binocular rivalry integrates several stages of the visual pathway, depending on the stimulus characteristic, paradigm and perceptual state.

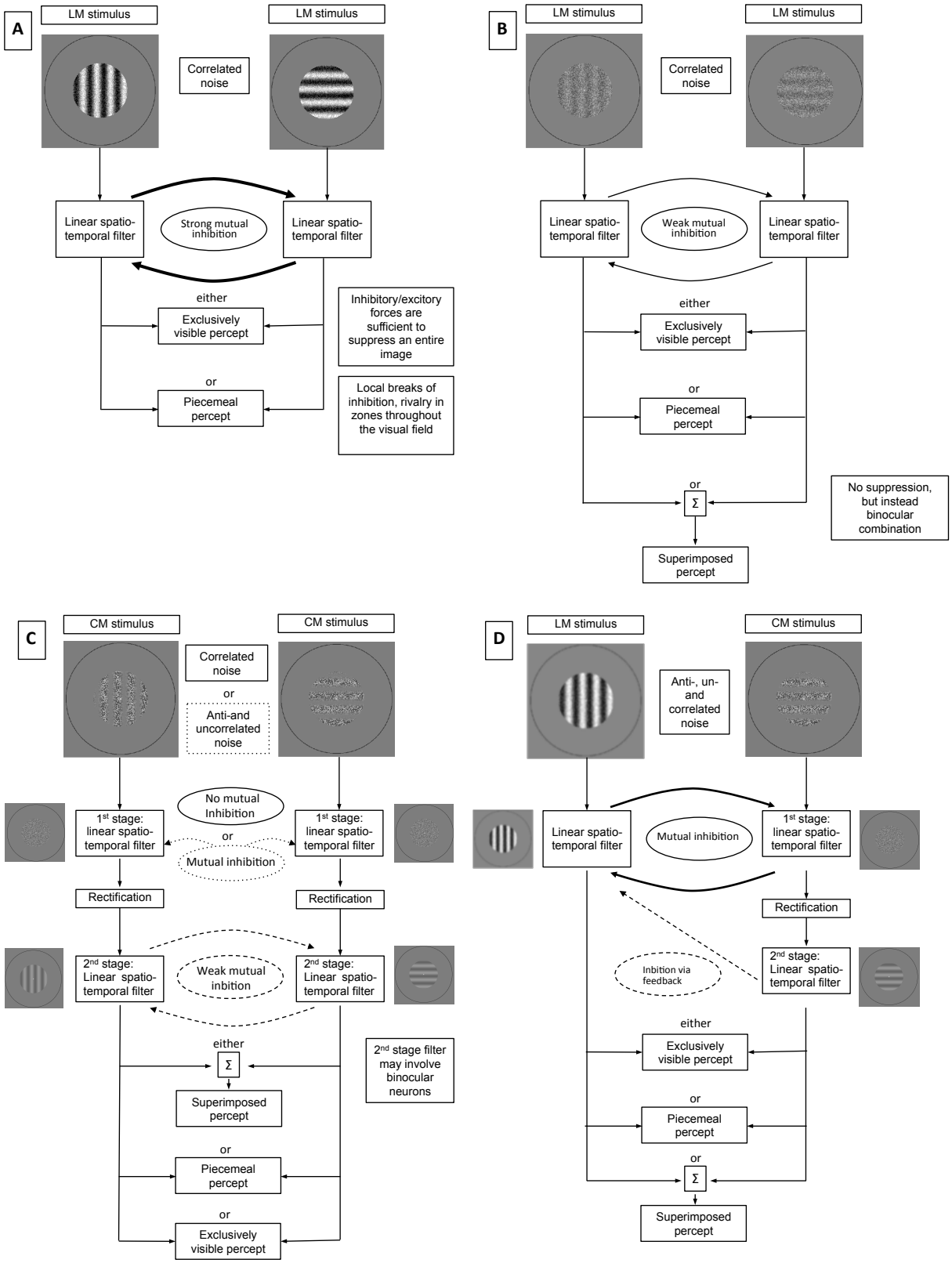

Figure 4.9: Model for LM and CM binocular rivalry. A) Traditional view of mutual inhibition between two competing high-contrast LM gratings. Monocular units respond with orientation and spatial-frequency selectivity to luminance variations. As the illustrated orientations are in interocular conflict, one percept will be perceived whilst the other will be suppressed. B) Low-contrast gratings are likely to be seen in a piecemeal or superimposed

fashion. The later state suggests an involvement of binocular neurones C) Model for CM binocular rivalry. The correlated noise-carriers, processed in the first filter stage, do not compete because the spatio-temporal luminance input corresponds between the eyes. The second filter stage engages thereafter in weak but significant binocular rivalry (see Section 2.7.3 Why is CM binocular rivalry different than LM binocular rivalry?). D) LM stimulus in competition with a CM stimulus. The LM spatio-temporal luminance input and the first filter stage of the CM stimulus are mutually inhibiting each other and additionally feedback signals from envelope encoding neurones are further suppressing the LM processing neurones.

4.6.2 CM versus LM: Perception across time

Previously, I have shown that when orthogonally orientated LM stimuli are presented dichoptically to the eyes, proportion of exclusive visibility increases during the first 9 s (see Section *2.5.3 Results*). There is a mild decrease of piecemeal and superimposed percepts for the same time window (see Section *3.3.3 Results of perception across time*). I suggested that the areas, receiving the initial input, tend to combine rather than suppress information, resulting in greater proportions of mixed states being perceived during the first few seconds. In contrast to the trend observed with LM stimuli, exclusive visibility for CM stimuli was constant across 120 seconds (see Section *2.5.3 Results*). In the first experiment of this chapter, I show that when a LM grating competes with an orthogonally orientated CM grating, exclusive visibility of the LM stimulus decreases whilst that of the CM one increases during the first 6 seconds of an experimental trial (Figure 4.4A). I hypothesise that the decline of exclusive visibility of the LM grating is due to a simultaneous increase of feedback signals from the envelope processing stage of the CM stimulus (Figure 4.8D). Also, the analysis revealed that the increase of exclusive visibility of the CM stimulus (Figure 4.4B) during the first seconds was accompanied with an increase of superimposition (Figure 4.4D). I suggest that the neurones, which process CM information, are also involved in processing binocular combination.

Whilst piecemeal perception tends to be stable throughout the trial duration, superimposition increases (Figure 4.4C and D). This result strengthens my hypothesis that the visual system inherently tries to combine information rather than engage in visual competition. Additional support for this idea comes from Klink and collaborators (Klink et al., 2010a, b) as they demonstrated that superimposed perception increased across time when noiseless luminance-

modulated stimuli were presented dichoptically whereas piecemeal perception did not change significantly.

4.6.3 CM versus LM: Distribution of perceptual states

The total number of exclusively visible events during binocular rivalry are typically best fit with gamma (e.g. Levelt, 1965, 1967; Lunghi and Burr, 2013) or lognormal functions (Lehky, 1995; Zhou, Gao, White, Merk, and Yao, 2004). Other multistable percepts distributions are also well fit with those functions (e.g. Kleinschmidt, Buchel, Zeki, and Frackowiak., 1998; Zhou et al., 2004; Pastukhov and Braun, 2008; O' Shea, Parker, La, and Alais, 2009), which has led to the suggestion that they have a common underlying processing mechanism with binocular rivalry. The coefficient of determination (R^2) has been used as a measure to compare actual data with a model fit and serves as an indicator of goodness of fit (e.g. Logothetis, Leopold, and Sheinberg, 1996; O' Shea et al., 2009; Lunghi and Burr, 2013). The results show that data can be fit with gamma functions and R^2 values are close to 1 for both exclusively visible CM and LM stimuli (Figure 4.5, top). The only atypical shape occurred when LM stimuli were presented at near contrast-detection threshold, which is likely at least in part to be due to very few exclusively visible events (Figure 4.2A).

The results for piecemeal and superimposition also follow gamma-like patterns with R^2 values that indicate solid goodness of fits (Figure 4.5, middle and bottom rows), except for the near threshold conditions, probably again, due to low numbers of events.

4.6.4 CM versus LM stimuli in light of Levelt's modified laws

When CM stimuli are competing with LM stimuli, the dynamics of binocular rivalry are not predicted correctly by taking into account the visibility levels, as described by Levelt's modified four laws (Figure 4.6). I suggested, in the model above, that the proposed differences in processing sites involved in extracting luminance- and contrast-modulated information are reflected in the characteristics of binocular rivalry when these stimuli compete with each other. I will now consider the results in light of Level's laws.

Based on the notion that multiples over detection threshold represent stimulus strength, the first modified law predicts that the LM stimuli should generate greater proportions of exclusive visibility accompanied by longer mean exclusivity duration (second modified law) when the visibility is greater than the visibility of the competing CM stimulus (Figure 4.6A and C). In fact, LM stimuli never reached predominance in exclusive visibility, not even when a highly visible LM stimulus (~ 43x) was competing with a less visible (~ 7x) CM stimulus. Levelt's modified third law would predict a decline in full flip rate when the difference between visibilities of the rivalrous stimuli increases (Figure 4.6E), however, the opposite was the case: the full flip rate (and all other perceptual changes) increased with increasing differences between visibilities (Figure 4.6F). An equal increase of both stimuli's visibilities should, according to Levelt's modified fourth law, lead to an increase in the numbers of full flips, but as the second experiment revealed (see Section *4.6. CM versus CM: Do Levelt's modified four laws hold when only CM stimuli compete?*), the increase in visibility did not significantly change the full flip rate (Figure 4.6G and H).

Levelt' modified laws	**L versus L (Brascamp et al., 2015)**	**LM versus LM (Results of the current thesis)**	**CM versus CM (Results of the current thesis)**	**CM versus LM (Results of the current thesis)**
First	✓	✓	✓	X
Second	✓	✓	✓	X
Third	✓	✓	X	X
Fourth	✓	✓	X	X

Table 4.2: Comparison of whether Levelt's modified four laws hold for various stimulus types. The check marks indicate that the laws hold for the specific conditions whereas the x' indicate that the modified law do not hold.

4.6.5 CM versus CM and LM versus LM stimuli in light of Levelt's modified four laws

When CM stimuli compete under binocular rivalry conditions and their visibilities are changed to replicate Levelt's modified four laws (see Section *4.6. CM versus CM: Do Levelt's modified four laws hold when only CM stimuli compete?*), the observed changes in binocular rivalry dynamics follow only the first and second modified laws (Figure 4.7A-D) whereas LM stimuli produced results in line with Levelt's modified four laws.

4.6.5.1 Why do rival CM stimuli generate results in line with the first and second, but not with the third and fourth modified law?

The first and second modified law describe changes of exclusive visibility and mean percept duration when the interocular differences of stimuli strengths are changed.

I have illustrated this in a three-well model (Figure 4.9), which I already used to describe the findings of the third chapter (see Section *3.4.5 Why do CM stimuli engage in much more superimposition than LM stimuli?*). Figure 4.9A and B depicts the stimulus conditions used in the third experiment of this chapter (visibility ~ 3.5x to one eye and visibility ~ 7x to the other eye) for LM (A) and CM stimuli (B). The left and right well-troughs represent exclusively visible perception whereas the middle troughs represents superimposed perception. The red ball indicates the actual perceptual state. The gradual grey-transient in the centre of each graph represents the area, in which piecemeal and superimposed perception arise.

The underlying neurones of the 'stronger' stimulus have the upper hand over the 'weaker' neurones in the context of mutual inhibition. I propose that this dynamic is irrespective of whether neurones are receiving initial monocular (first-order) or initial binocular (second-order) input (depth of left and right wells are the same for LM and CM stimuli). Following this idea, a 'stronger' stimulus within the LM (Figure 4.10A) and CM (Figure 4.10B) processing system will generate predominately exclusive visibility (first modified law) and longer mean exclusivity durations (second modified law). However, whilst a unilateral change of visibility level (third modified law) or a bilateral change of visibility level (fourth modified law) will change perceptual alternation for LM stimuli (Figure 4.10C), it will not significantly change the number of perceptual alternations for CM stimuli because of the greater proportions of superimposition for CM compared to LM stimuli (Figure 4.110D). This

is due to the underlying CM-processing neurones, which combine information rather than engage in competition (see Figure 4.9C and also *Chapter 2* and *3*).

It has been shown that an increase of visibility level via a change in contrast leads to a decrease of superimposition for L stimuli (Liu et al., 1992; Brascamp et al., 2006), which also applies to LM stimuli as shown in Figure 4.8A (fourth modified law). Surprisingly, CM stimuli generate greater proportions of superimposition when the visibility levels of both eyes equally increase (Figure 4.8B). However, this result again indicates that CM stimuli rarely alternate abruptly from one exclusive state to the other. It also implies that an increase of bilateral visibility level or 'stimulus strength' for CM stimuli increases binocular combination rather than exclusive visibility and binocular rivalry alternation.

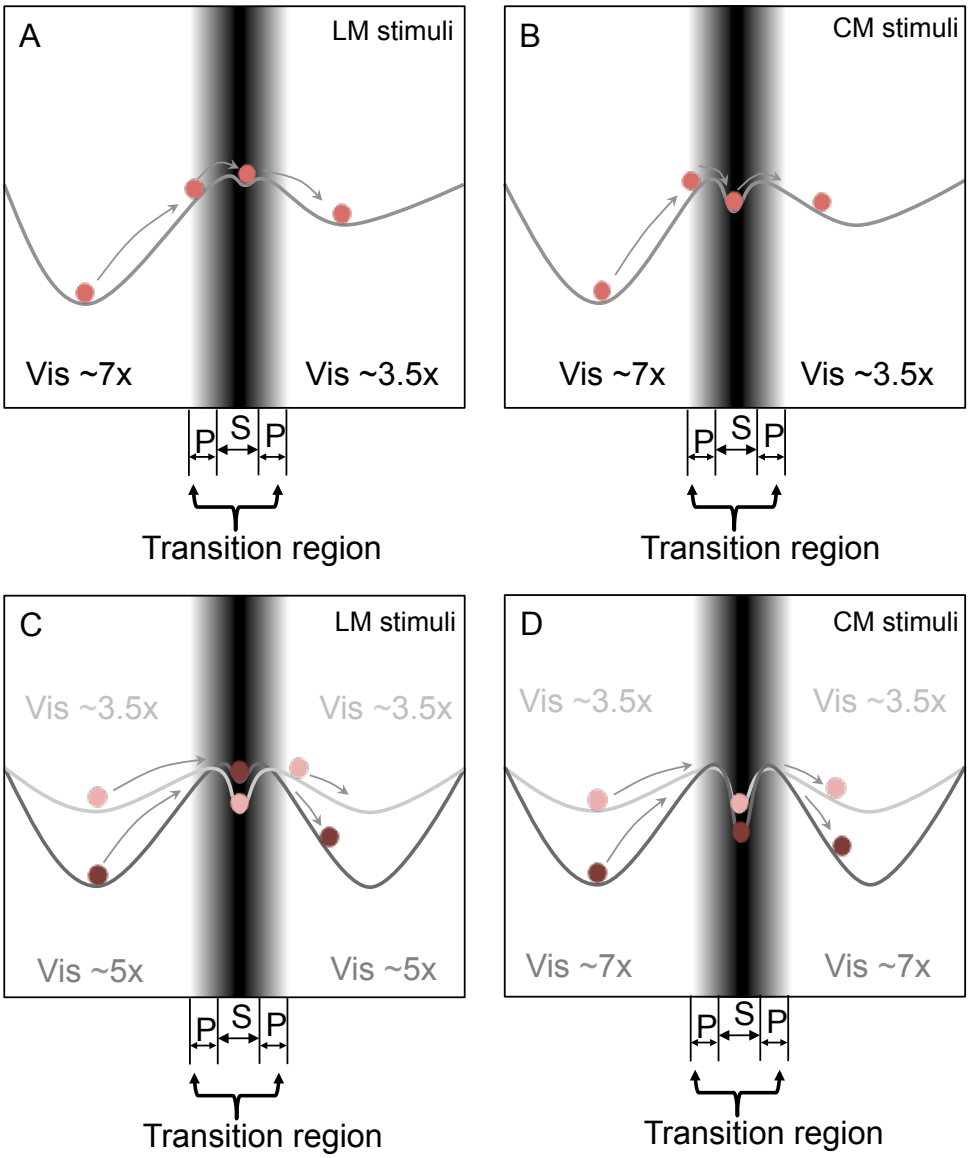

Figure 4.10: Three-well scheme introduced in Chapter 3 to describe the effect of uni- and bilateral variations of visibility *levels for LM and CM stimuli. The stimulus conditions used in the third experiment of this chapter (*visibility *~ 3.5x to one eye and* visibility *~ 7x to the other eye) for LM (A) and CM stimuli (B). The left and right well-troughs represent exclusive visibility whereas the middle well represents superimposition. The red ball shows the actual perceptual state. The grey transition in the centre of each graph represents the area that generates piecemeal and superimposition. The light grey lines indicate* visibility *~ 3.5x and the dark grey* visibility *~ 5x for both LM stimuli (C) whereas the light grey lines indicate* visibility *~ 3.5x and the dark grey* visibility *~ 7x for both CM stimuli (D).*

4.7 Conclusion

LM stimuli never reach predominance over competing CM stimuli, even if the visibility of a LM stimulus is far above that of the competing CM stimulus. The results presented in this chapter also showed that Levelt's modified four laws fail to predict the perceptual course when LM and CM are in competition and only hold for the first and second modified law when CM stimuli compete with each other. When a CM stimulus is in competition with an LM stimulus under binocular rivalry conditions, the analysis of this chapter did not corroborate Levelt's modified laws, indicating a strong psychophysical evidence for separate processing mechanism for CM and LM. Moreover, bilateral increase of CM's visibility levels tend to increase superimposition, which suggests that the visibility level increase engages the underlying binocular neurones into combination rather than competition. I concluded that next to the stimulus strength or visibility level, the stimulus type and its underlying processing site are important factors determining perception during binocular rivalry. Finally, I proposed a model for LM and CM binocular rivalry, which addresses the different psychophysical results and their underlying processing sites.

Chapter 5 - Summary of the results and conclusion

The aim of this thesis was to investigate binocular rivalry characteristics when using LM and CM stimuli. In all experiments, binocular rivalry was initiated by presenting orthogonally orientated sinusoidal gratings dichoptically to the eyes. The following sections summarise the main findings of each experimental chapter as well as attempts to place the knowledge about CM binocular rivalry that was generated by this thesis in a wider context. The last section discusses prospects for future research concerning CM binocular rivalry.

5.1 The influence of stimulus visibility and size on rivalrous LM and CM stimuli

In the first study (*Chapter 2*), I compared binocular rivalry characteristics of L, LM and CM gratings (LM and CM using inter-ocularly correlated noise). L and LM stimuli generate many more perceptual alternations and greater proportions of exclusive visibility than CM stimuli, even when the visibility was comparable. This implies that CM stimuli were mainly perceived as a mixed percept. Also, it is known that an increase of stimulus size for L stimuli generates greater proportions of mixed perception (e.g. Blake et al., 1992; O'Shea et al., 1997). The same effect was found for LM and CM stimuli.

5.1.1 Monocular grid versus binocular rivalry condition

The low proportions of exclusively visible percepts and the lower number of perceptual alternations for CM stimuli with correlated noise found in first study of this thesis (see *Chapter 2*) could be explained not by binocular rivalry related mutual inhibition of competing neurones, but instead by attention shifts or local adaptation. I addressed this question by carrying out an additional experiment, in which a CM or LM grid was presented to one eye, whilst the other eye perceived a noise stimulus. The participants were unaware of the purpose of this experiment and were instructed to indicate exclusive visibility of a vertical or horizontal grating, or mixed perception. Using comparable visibility levels for LM and CM stimuli, a comparison of these experimental results with those from conventional binocular rivalry was carried out. CM stimuli did generate significantly more exclusive visibility under binocular rivalry than under CM grid conditions, implying that it is very likely that the CM binocular rivalry is due to actual binocular rivalry alternation. This indicates that binocular rivalry initiated with CM stimuli is due to a mutual inhibition process.

5.2 The contribution of piecemeal and superimposition to perception of rivalrous LM and CM stimuli

The first experimental chapter revealed greater proportions and longer phases of mixed perception for CM, compared to LM stimuli (see *Chapter 2*). When using identical spatial frequencies, mixed perception can occur in a piecemeal or superimposed fashion. Whilst piecemeal perception was described as rivalry in local areas across the visual field (Blake, O'Shea and Mueller, 1992), superimposition indicates binocular combination (e.g. Liu et al., 1992; Brascamp et al., 2006; Klink, Brascamp, Blake and van Wezel, 2010a; Klink, Brascamp, Blake and Wezel, 2010b). The four-alternative-forced-choice task used in *Chapter 3* and *Chapter 4* takes into account dynamic changes of exclusive visibility of either a horizontal or vertical grating, piecemeal and superimposed percepts across a trial. To the best of my knowledge, this paradigm has not been used before. I revealed in *Chapter 3* that CM stimuli, regardless of any manipulations to interocular noise configuration, engaged in significantly more superimposition than comparable LM stimuli did. These results are in line with those emerging from other studies concerning second-order stimuli, in which the authors suggested that CM stimuli are at least partially processed in visual areas, which are initially receiving binocular, rather than monocular input (e.g. Wong et al., 2001; Chima et al., 2015).

Piecemeal perception was not significantly affected by variations of interocular noise configurations. Interestingly, within 'piecemeal perception' category, participants reported the occurrence of a perceptual state, which contained portions of both superimposed and piecemeal perception (see Appendix *6.2 Current and modified view on perceptual states during binocular rivalry*). This perceptual state has not been described previously. I suggested that this 'bridge state' is in line with Brascamp et al.'s (2006) idea of a gradual evolution of binocular rivalry states, meaning gradual transitions between exclusive visibility, piecemeal and superimposition (see *Chapter 3*).

5.3 The influence of interocular noise configuration on rivalrous LM and CM stimuli

In *Chapter 3* I investigated the effects of different interocular noise correlations on binocular rivalry. The results of previous studies concerning second-order stimuli did not show any significant influence of noise configurations (Wilcox and Hess, 1996; Georgeson and Schofield, 2011; Zhou et al., 2014; Zhou, Georgeson and Hess, 2014). For binocular rivalry, however, un- and particularly anti-correlated noise provides additional potential to rival as an incompatible stimulus characteristic (i.e. noise checks corresponding in time, space, but not in luminance) is a signature to initiate binocular rivalry. And indeed, anti- and uncorrelated noise configurations generated significantly greater proportions of exclusive visibility than correlated noise configurations for both LM and CM stimuli. On the other hand, the proportions of piecemeal perception were not significantly affected by variations of the noise configurations. I suggested that the rivalrous noise pages add to the competition of the orthogonally orientated envelopes of the CM stimuli.

5.4 Different processing sites for LM and CM stimuli

Previously, authors of second-order stimuli studies suggested different processing mechanisms for first-and second-order stimuli (e.g. Schofield and Georgeson, 1999; Baker and Mareschal, 2001; Landy and Graham, 2004; Sukumar and Waugh, 2007; Chima, Formankiewicz and Waugh, 2015). *Chapter 2* and *Chapter 3* revealed that even under comparable visibility conditions, binocular rivalry metrics of CM stimuli are very different to those of LM stimuli. *Chapter 4* demonstrated that Levelt's modified laws, which predict perceptual characteristics during binocular rivalry, fail when a CM stimulus competes with a LM stimulus. Thus, I conclude that the results presented in all three experimental chapters are in line with the idea of different processing sites for CM and LM stimuli.

Some studies concerning second-order stimuli suggested an involvement of binocular neurones during initial processing of second-order stimuli (e.g. Wong et al., 2001; Chima et al., 2016). *Chapter 3* showed that CM stimuli engaged significantly more in superimposition than comparably visible LM stimuli. Superimposition is an indicator of binocular combination rather than binocular rivalry and was suggested to be processed initially by binocular

neurones (e.g. Liu, Tyler and Schor, 1992; Brascamp et al., 2006; Klink et al., 2010a). Hence, I support the idea of an initially binocular processing site of CM stimuli.

5.5 CM stimulus conditions in the light of Levelt's modified four laws

Levelt's modified four laws describe the influence of visibility on the perception during binocular rivalry of first-order stimuli. *Chapter 4* demonstrated that a LM stimulus does not predominate perception when competing with a CM stimulus, even if the visibility level of the LM stimulus is many times above that of the CM stimulus.

The increase of bilateral stimulus visibility tends to increase the proportions of superimposed perception for CM stimuli whereas it decreases superimposition for LM stimuli. Also, when a CM stimulus competes with an LM stimulus during binocular rivalry, exclusive visibility of the CM stimulus as well as superimposed perception, both increase during the first few seconds. This result suggests that the neurones that are responsible for initially processing CM stimuli are also processing binocular information.

I revealed that Levelt's modified laws only hold under certain stimulus conditions and that, in addition to stimulus strength, the stimulus type (CM or LM) must be taken into consideration to correctly predict the characteristics of binocular rivalry. Finally, I developed a model that addresses the different characteristics of LM and CM binocular rivalry.

5.6 A binocular rivalry model concerning luminance- and contrast-modulated stimuli

One of the main findings of *Chapter 2* indicated lower proportions of exclusive visibility for CM compared to LM stimuli. In *Chapter 3* I reported that CM stimuli, regardless the interocular noise configuration, engage in significantly more superimposition than LM stimuli. I modified existing double well models (Brascamp et al., 2006; Pastukhov and Braun, 2008) to develop a theoretical framework, which helps to explain those perceptual differences by firstly including piecemeal and superimposition into these models. Secondly, I introduced a third well to this model, which represents superimposition (resulting in a 'threefold well model'). Thirdly, I differentiated between LM and CM models by implementing a deeper well

for superimposition for the CM model, which addresses the greater proportions and longer phase of superimposition as well as the greater number of reversions within mixed states for CM compared to LM stimuli.

In *Chapter 4*, I demonstrated that LM stimuli fail to predominate perception when competing with CM stimuli under binocular rivalry conditions, even if the visibility of the LM stimulus was many times above that of the CM stimulus. Firstly, I connected current models of LM and CM processing (e.g. Baker and Mareschal, 2001; Georgeson and Schofield, 2011) with recent models concerning binocular rivalry (e.g. Tong, Meng and Blake, 2006; Seely and Chow, 2011). Then, I developed a model, which explains exclusive visibility and piecemeal perception as a result of mutual inhibition between first-order processing neurones whereas superimposed perception, as an indicator for binocular combination, is initially processed by binocular neurones. The next step was to apply the concept to CM stimuli, which are suggested to be processed in two stages (e.g. Schofield and Georgeson, 1999; Baker and Mareschal, 2001). The first stage processes the carrier information whereas the second stage, the envelope information of a CM stimulus. In my model, the first stages engage only in mutual inhibition if the interocular noise is non-correlated. The second 'envelope-processing' stage however engages in mutual inhibition regardless of noise configuration. If a CM and an LM stimulus compete under binocular rivalry conditions (*Chapter 4*), then mutual inhibition between the carrier stage of the CM and the monocular grating processing stage of the LM stimulus arises. I suggested that feedback signals from the envelope stage of CM stimuli causing predominance of CM stimuli when competing with similarly visible LM stimuli. Finally, I used the three-well-model to explain why competing CM stimuli only follow Levelt's first and second, but not third and fourth modified laws.

5.6.1 Is there a common processing mechanism for LM and CM binocular rivalry and other multistable percepts?

Some researchers have attempted to include all multistable percepts in a unifying model (e.g. Sterzer, Kleinschmidt and Rees, 2009; Scocchia, Valsecchi and Triesch, 2014) since it has been shown that they share some characteristics, namely distribution of dominance phases, which are well fit by gamma functions (e.g. De Marco, Penengo and Trabucco, 1977; Sterzer, Russ, Preibisch and Kleinschmidt, 2002; Zhou et al., 2004), alternation rate variations due to variations of stimuli sizes and colours (O' Shea et al., 2009) and some similarities in

metabolic activity (Knapen et al., 2011; Buckthought, Jessula and Mendola, 2011). However, the depth of suppression was found to be different across various multistable percepts (e.g. Tsuctshiya, Koch, Gilroy and Blake, 2006; O' Shea et al., 2009).

The development of a common underlying processing mechanism even within binocular rivalry remains rather difficult. As the hierarchy in Figure 5.1 demonstrates, knowledge of the stimulus-presentation-paradigm, the stimulus type, the complexity of the stimulus and the perceptual state are critical before making any suggestions of an underlying processing site of any multistable percept.

How do the results for CM binocular rivalry then fit into a wider model of multistable percepts? In this thesis, I revealed that LM and CM binocular rivalry show significant differences in various metrics and have suggested that exclusive visibility of second-order stimuli may be the result of competition between interocular luminance noise (carrier) processing neurones (first-order) and competition between grating (envelope) processing neurones (second-order). If those second-order processing neurones are orientation selective (as suggested by results of animal single cell studies (An et al., 2014; Li et al., 2014)) and receive predominately binocular input (as suggested by e.g. Chima, Formankiewicz and Waugh, (2015) and Wong, Levi and McGraw, (2001)), then they could also serve as a source for alternation between dominance phases during monocular rivalry. It remains unclear at this point of research whether other multistable percepts involve those second-order processing neurones as well.

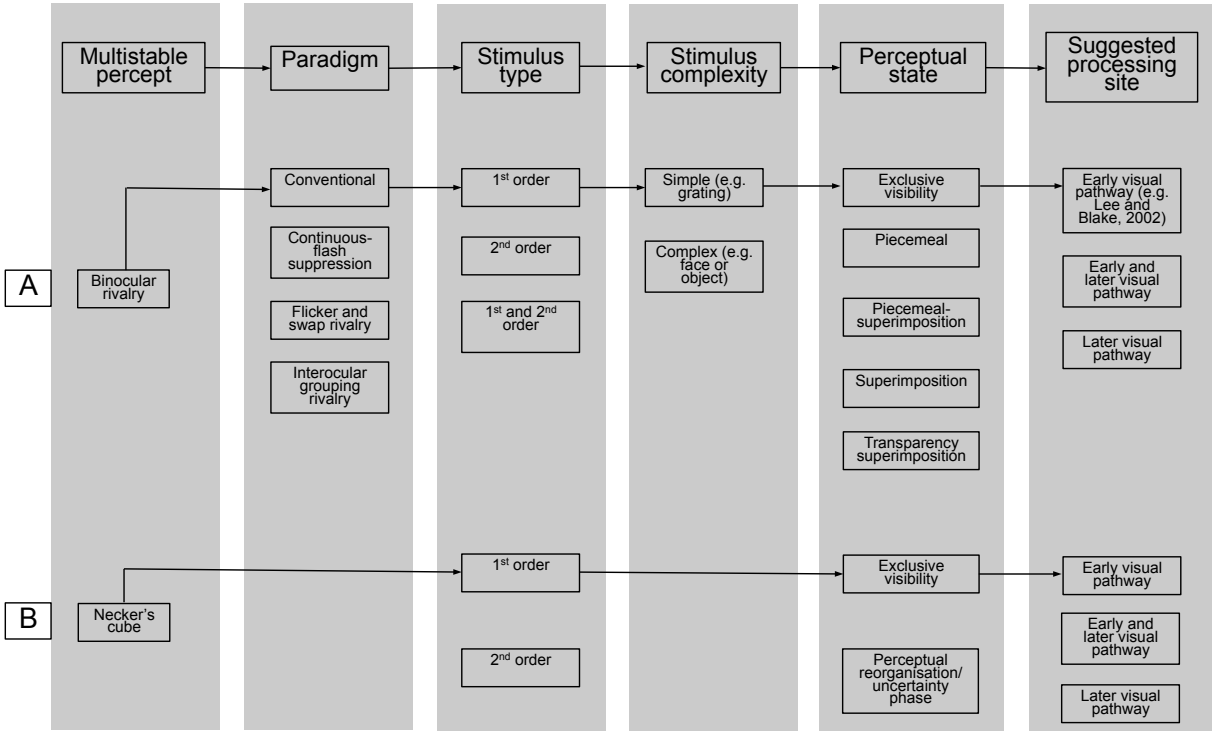

Figure 5.1: Scheme of the link between multistable percepts and their underlying processing site. Note that the suggested processing sites are simplified. Specific brain regions could be used instead (i.e. LGN, V1, V2 etc.) The arrows follow for simplicity only one particular case. A) Example binocular rivalry. B) Example Necker's cube.

5.7 Future work

The insights gained from binocular rivalry research indicate a number of gaps in the existing literature, which should be addressed by future research projects that could deepen our understanding binocular rivalry when using second-order stimuli. Second-order refers by definition to stimuli "...whose principal attributes are defined by variations in contrast or texture." (Baker and Mareschal, 2001, page 17). It is important to understand whether texture-defined stimuli demonstrate the same properties as CM stimuli do. Perceptual difference generated by different second-order stimuli may help to understand the processing hierarchy within the visual system.

As mentioned earlier in this chapter, other multistable objects alternate between different perceptual states (see Section *5.5.1 Is there a common processing mechanism for LM and CM binocular rivalry and other multistable percepts?*). Those multistable objects, e.g. Necker's cube, trigger flips between perceptual states even when they are seen with one eye only,

implying an initial process site, in which pattern representations compete. Thus, higher cortical levels may be involved than those that process exclusive visibility during binocular rivalry. The question is whether binocular rivalry metrics such as alternation rate would be the same between LM and CM stimuli, considering the idea established in this thesis and elsewhere (e.g. Wong, Levi and McGraw, 2001; Sukumar and Waugh, 2007) pertaining to initially binocular processing site for CM stimuli.

In this thesis, I used the conventional binocular rivalry paradigm to initiate perceptual competition, i.e. with static orthogonally orientated gratings, dichoptically presented to the eyes. As reported in the literature review, binocular rivalry can also be provoked by meaningful stimuli like objects or faces. A comparison between meaningful LM and CM stimuli might help gaining deeper insight into processing of first- and second-order stimuli.

Moreover, Diaz-Caneja's (1928) (translated by Alais, O'Shea, Mesana-Alais and Wilson (2000)) and Kovács et al.'s, (1996) interocular grouping paradigms as well as Logothetis et al.'s, (1996) flicker-swap-rivalry paradigm demonstrated various other ways of initiating perceptual exclusivity, which may arise from different visual areas than those initiated by conventional binocular rivalry. As hypothesised for multistable objects, a comparison between CM and LM stimuli under those conditions may reveal no significant differences between stimulus types, assuming these special cases of exclusive visibilities are processed initially in the same binocular brain regions as those processing initially CM stimuli. Preliminary results of a study concerning interocular grouping of LM and CM stimuli suggest different binocular rivalry properties for those stimulus types and common underlying processing sites for both exclusive visibility generated by conventional binocular rivalry conditions and percepts generated by an interocular grouping paradigm (see Appendix *6.4 Preliminary results: Interocular grouping generated by luminance- and contrast-modulated stimuli*).

Finally, binocular rivalry has been used as a tool to conduct several clinical research projects (see Section *1.2.2.4 Clinical applications for mixed perception during binocular rivalry*). Particularly amblyopes stands out, as it has been shown that the relative loss of detection sensitivity is greater for CM than LM stimuli in amblyopic eyes. Hence, amblyopes may show different characteristics of CM binocular rivalry than a control group with normal vision.

Appendix

6.1 Stimulus calibration

Each CRT monitor inherently produces pixel luminance values, which differ from the intended pixel luminance value due to non-linear voltage output. Gamma correction is therefore necessary to calibrate the monitor to generate the intended pixel luminance value.

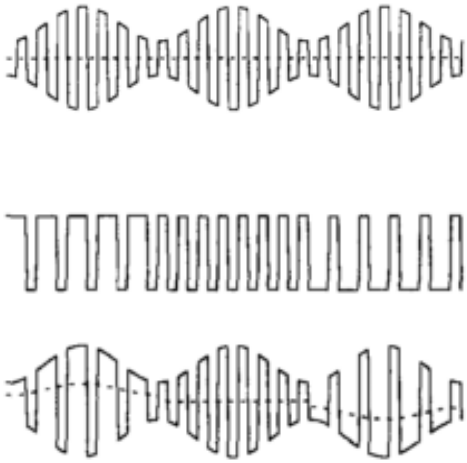

Figure 6.1: Scheme of various noise pixel mean luminance profiles. Top: Mean luminance profile (dotted line) across a stimulus profile (straight line) with equal numbers of light and dark pixel. Middle: A noise pattern (shown as a regular wave form for simplicity) with overall equal numbers of light and dark pixels, however in the first segment there are twice as many light pixels as dark, in the middle segment there is no bias and in the last segment there is the opposite bias. Bottom: These local variations lead to variations of the overall mean luminance profile (dotted line) (Smith and Ledgeway, 1997).

The actual luminance value of adjacent pixels is unequal to the intended values and thus leads to a variation of local mean luminance (Figure 6.1). This so-called adjacent pixel non-linearity (APNL) (Klein, Hu and Carney, 1996) causes another first-order artefact in the second-order stimuli. As Figure 6.2 (left) shows, in the transient area between a dark and a light pixel, the actual luminance (dashed line) is much lower than the intended one (straight line). The next transition from a light to a dark pixel shows a slight discrepancy between actual and intended luminance. These differences between intended and actual luminance for each pixel will cause a lower mean luminance level than anticipated. This luminance profile is a reflection of the voltage change of a CRT display's video amplifier, which generates the pixel (Figure 6.2 right).

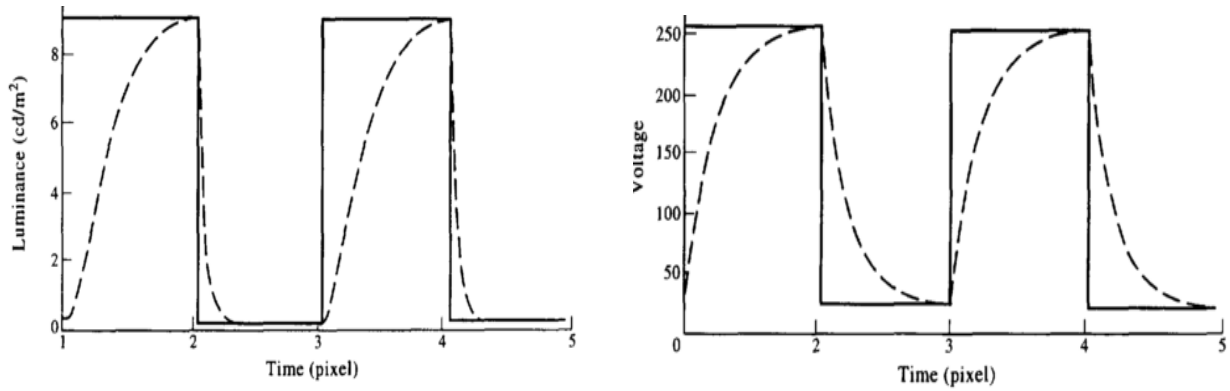

Figure 6.2: Luminance and voltage profile of 4 neighboured light and dark pixel. Left: The solid line shows the intended luminance profile of white and black pixel. The dashed line shows the actual luminance profile. The mean luminance of the actual result is lower compared to the planed profile. Right: The solid line shows the intended voltage profile of white and black pixel. The dashed line shows the actual voltage profile (Klein et al., 1996).

Psychophysical evidence from a study by Manahilov, Calvert, and Simpson (2003), in which the participants had to carry out a discrimination task, using LM and CM gratings. The researchers compared threshold when using a small (2 x 2 min of arc) and big pixel size set up (8 x 8 min of arc). The results revealed that the thresholds for LM gratings of large sized noise were significantly higher than the thresholds in the presence of small sized noise whereas such difference could not be shown for CM stimuli. Therefore, the noise pixel size only influences LM but not CM perception. Moreover, keeping the luminance difference (i.e. pixel to pixel contrast) small minimizes the effect of APNL as well (Klein, Hu and Carney, 1996). One way of reducing the effect of APNL is to group pixels of the same luminance 'checks' so that APNL affects fewer pixels (Figure 6.3).

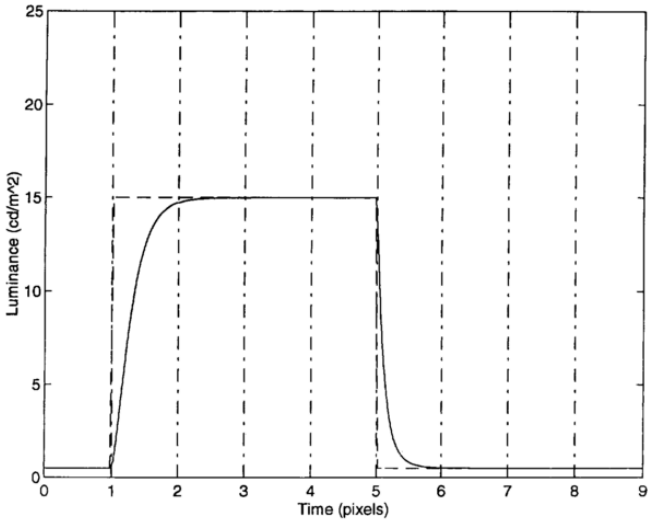

Figure 6.3: Luminance-profile of four adjacent dark and 4 light pixels. The horizontally dashed line shows the intended luminance profile. The horizontally solid line shows the actual luminance profile. The luminance profile does not follow the intended luminance at the transient areas of the pixel check but in the centre (Klein et al., 1996).

6.2 Current and modified view on perceptual states during binocular rivalry

Figure 6.4 depicts the current and modified view on perceptual states, which can arise when orthogonally presented gratings of the same size and spatial frequency separately to the eyes. The modified view incorporates a percept that contains portions of piecemeal and superimposition. These scheme based on reports from individuals, which participated in experiments of the third chapter.

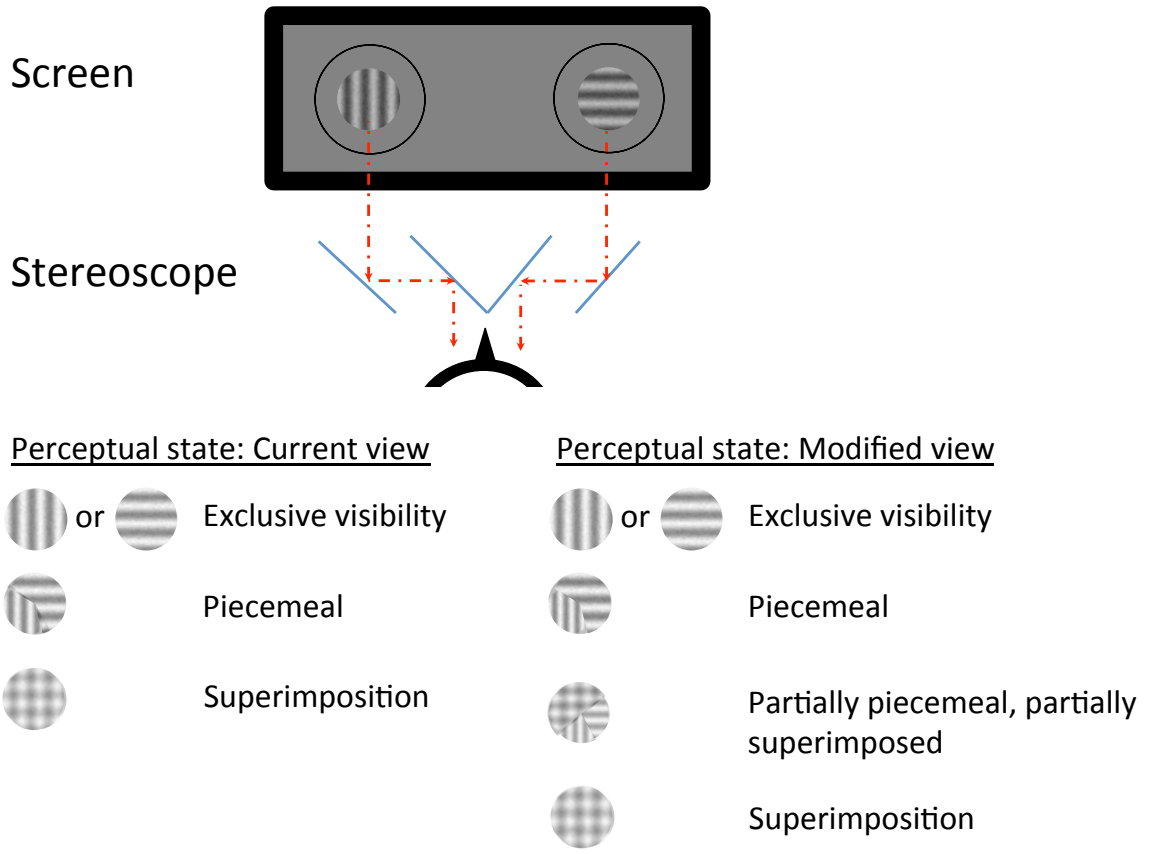

Figure 6.4: Scheme of current and modified perceptual states during binocular rivalry initiated by gratings of the same size and spatial frequency. The example perceptual states shown are generated by L stimuli.

6.3 Luminance profiles for LM and CM stimuli

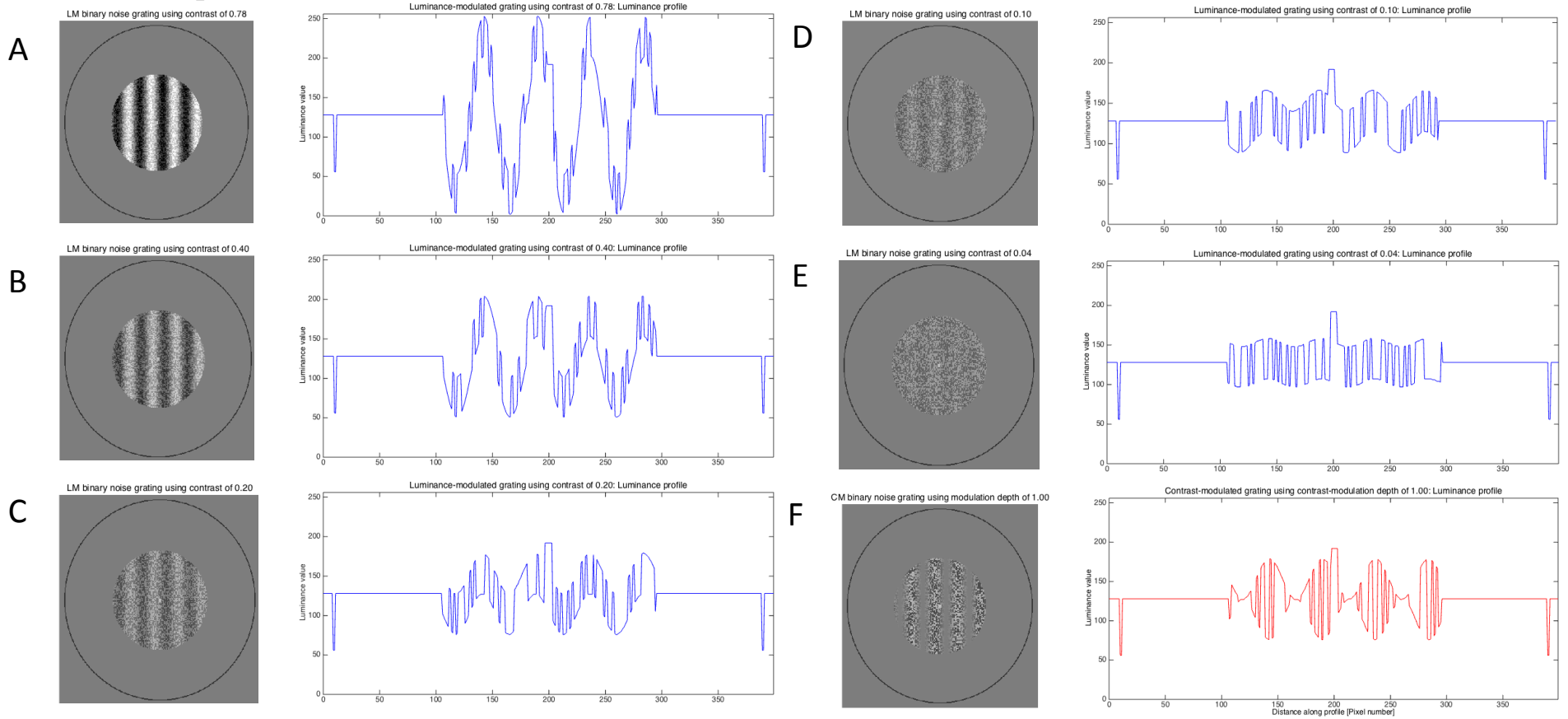

Figure 6.5: Illustration of Chapter 4's vertical LM and CM gratings with luminance profiles for a horizontal line of pixels through the centre of the stimulus. A-E) LM sinusoidal grating with contrast of 0.78 (A), 0.40 (B), 0.20 (C), 0.10 (D), 0.04 (E) and added two-dimensional binary noise with a contrast of 0.20. F) CM sinusoidal grating with a two-dimensional binary noise carrier, which had its contrast modulated by the grating (modulation 1.00). Both stimuli were surrounded by a fusion lock of a 4 deg diameter and contained a static fixation spot (size of 6x6 pixels) in the centre with a luminance contrast of 0.20.

6.4 Preliminary results: Interocular grouping generated by luminance- and contrast-modulated stimuli

Preliminary results of an experiment concerning interocular grouping generated by LM and CM stimuli were presented in a poster at the ECVP conference 2016 in Barcelona (Spain).

Investigations of inter-ocular grouping for luminance- and contrast-modulated stimuli

Rivalrous luminance stimuli (L) presented dichoptically, each containing parts of two images, can generate periods during which one image is perceived due to inter-ocular grouping (IOG) or processing beyond the monocular level. We investigated the effects of different stimulus visibility level on IOG using L and luminance-modulated noise (LM) stimuli and compared the results with those of contrast-modulated noise (CM) stimuli.

Rivalrous grating stimuli, 2 deg in diameter, were constructed such that half of each contained a horizontal, and the other half a vertical, 2 c/deg sinusoid. Contrasts for L-and LM-stimuli were 0.98, 0.08, 0.03 and 0.78, 0.10, 0.06, respectively. The contrast-modulation depth for CM-stimuli was 1.00. Participants had to indicate whether exclusive horizontal or vertical IOG, superimposed, or any other percept, was seen.

IOG for L- and LM-stimuli was perceived proportionally more [$p<0.05$] for all contrast conditions compared to CM-stimuli. Decreasing L and LM contrast led to an increase of IOG. CM-stimuli produced mainly superimposed percepts, suggesting binocular combination rather than IOG. The results suggest different initial processing sites for IOG and superimposition as well as a predominately binocular processing site for CM compared to L- and LM-stimuli.

Figure 6.6: Abstract for a poster presentation at the ECVP conference 2016 in Barcelona, Spain.

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